Mechanisms that allow coexistence of three closely related species of predatory beetle

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This work is dedicated to my family; all of them.

DECLARATION

I declare that this is my own unaided work unless specifically acknowledged in the text. It has not been submitted for any degree or examination in any other university.

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Statistical notes and abbreviations

The following packages were used for statistical analyses.

Statistica for Windows Ver 4.5

Rudestat, Lighton 1994

Statgraphics Ver 4.0

Systat for Windows Ver 5.02

The following terms are used in the text:

d.f.	degrees of freedom
°C	degrees Centigrade
cm	centimetre
g	gram
hr	hour
mm	millimetre
µm	micron
n	sample size
n.s.	not significant at 95% level
P	probability
r^2	coefficient of determination; least squares regression
r_s	rank correlation coefficient
s	second
s.d.	standard deviation
s.e.	standard error
♂	male
♀	female

ABSTRACT

The rove beetles *Philonthus (Spatulonthus) incognitus* Boheman, *Philonthus (Spatulonthus) labdanus* Tottenham and *Philonthus (Spatulonthus) sanamus* Tottenham (Coleoptera: Staphylinidae) were found to co-occur throughout a large expanse of Africa, apparently coexisting in the same habitat. The biology of the three species was investigated to establish the extent of this co-occurrence, and to explore the mechanisms, if any, by which these three species coexist.

All three species are closely related, overlap in their size ranges, and visit cattle dung, where they feed, lay their eggs and develop. The beetles were found to recognise only their own species as potential mates. This behaviour was used to verify the specific status of the beetles.

Museum collections were used to map the large scale distribution of *P. incognitus*, *P. labdanus* and *P. sanamus*. A transect of three sites, separated by approximately 100 km distance and 320m altitude, was sampled to measure the occurrence of the beetles in time and space. The species overlapped in their spatial and temporal distributions, from a continental scale, down to microhabitat selection, and seasonal to successional position, respectively. Both intra- and interspecific aggregation of adults was found in the field, which could potentially facilitate coexistence.

Evidence of character displacement, as a result of intraspecific competition, was looked for by examining the physiology, life history and morphology of *P. incognitus*, *P. labdanus* and *P. sanamus*.

The thermal biology (rate of development, developmental zero, and upper lethal temperature), of the three beetles revealed few differences between the species. Those differences that were found matched the gross distributions of the species, and could therefore most easily be attributed to environmental or phylogenetic constraints, rather than character displacement.

Examination of life history traits of the three species revealed similarities rather than differences, and the rapidly changing dung habitat is concluded to have been the overriding influence on the evolution of these traits.

Evidence of a competitive effect between *P. incognitus*, *P. labdanus* and *P. sanamus* was found in mixed-species rearing trials in the laboratory. Interestingly, laboratory bred beetles were found to be exceptions to the "developmental temperature - size rule", being larger rather than smaller when reared at elevated temperatures. However, no evidence of character displacement was found in the morphology of field collected specimens.

It is concluded that interspecific competition has not been the major influence in the evolution of the biology *P. incognitus*, *P. labdanus* and *P. sanamus*, and that no specific mechanisms for coexistence of the three species have evolved. It is proposed that the patchy and ephemeral nature of the dung habitat has caused a convergence, rather than divergence, in the life histories of the three species.

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CHAPTER ONE

GENERAL INTRODUCTION:

Community Structure and Competition.

1.1 The rationale for the study

If a community is defined as an assemblage of interacting species, then all organisms can be said to be living in communities. Despite nearly ninety years of considerable ecological investigation, the mechanisms of how communities are formed and how they are maintained is still open to debate. The two main candidates are coevolution mediated through competition, or allopatric speciation and stochasticity. One of the persisting challenges to ecology is to find species that are really coexisting and reveal the means by which they are achieving that coexistence (Gotelli, 1997; Young *et al.*, 1997). Close examination of such groupings at as many scales as is possible should hopefully give some clues as to which is the more probable route by which the species in question have come together and remained in some sort of equilibrium.

By looking at three closely related beetle species that occur in the same habitat, this study aims to find out if they are really coexisting. If so, how is this achieved? And finally, it attempts to explain the origin of this association as the result of interspecific adaptation or historical events.

Insects are the earth's most common type of organism (May, 1988) and most terrestrial communities are dominated by insects and green plants (Claridge, 1987). These communities show some consistent trends over time and space (Schluter and Ricklefs, 1993; Menge and Olsen, 1990; Ricklefs, 1987) and are commonly hierarchical (Rahel, 1990). Where does one start to examine these

patterns? How big or how small should the scope of any investigation be? "Not too big and not too small" (MacArthur, 1972) results in the Goldilocks response of Wiens (1984), who in agreement with Levin (1992), suggests there is no single natural scale at which ecological phenomena should be studied, rather examination at several scales will result in a study which is "just right". The scale at which a community is viewed can alter the conclusions made; abundance can vary from absolute measures through abundance rank to presence or absence. Consequently community patterns should be analysed and interpreted at more than one level, because the key to understanding lies in the elucidation of underlying mechanisms which operate at different scales (Levin, 1992).

1.2 Community structure

Just as communities can be examined at different scales, they can also be described in various ways. On different scales of spatial organisation, the first level is the individual habitat unit, in this case the dung pat, in which a number of species may be found, either as adults or a single larval generation. In this habitat there is the potential for interaction between the species and between the two major guilds of coprophages and predators. The microhabitat cannot be seen as part of the guild because the dung pat takes no active role in the interaction and is not seen to defend itself, although there may be some two-way effect between the microbial population and the insects (Hanski, 1987).

The next level of community organisation can be applied to the assemblage of local dung dwelling beetles. This is more inclusive in terms of species numbers, but patchy in that each species might not be present in each dung pat.

Finally, the regional or global set of species associated with cattle dung can be described and compared across continents, and compared with the other better studied coprophagous guilds sharing that habitat.

Two opposing schools of thought respond to the origin of such guilds with either the reaction that their existence is due to chance events and species are generally leading independent lives (Andrewartha and B'rch, 1954; James and Boecklen, 1984); and that it is unrealistic, given the allopatric origin of individual species in a community, to expect that the community will be organised (Walter *et al.*, 1984; Walter and Peterson, 1994). The other extreme is represented by assembly rules (Drake, 1990), which supposedly dictate the manner in which a community can form. Part of the problem in describing communities is the notion of the "balance of nature", with the world sitting comfortably at or near equilibrium, which is unlikely given the increasing biological diversity revealed by geological history (Rohde, 1997). The solution may lie in the middle ground, as the history of ecology shows that intermediate positions are often the most tenable (Price, 1984), and that it is not unreasonable to suspect that communities and guilds are not entirely random assemblages of species (Arthur 1987). Among a list of proposals, Wiens (1984), feels that an either - or - classification, such as equilibrium or non-equilibrium descriptions of community patterns is incorrect and suggests rather that ecological systems should be placed on a gradient. Dung dwelling staphylinids are probably closer to the non-equilibrium classification, while the ball-rolling scarabs, being apparently governed by biotic interactions (Hanski, 1991) may be closer to the equilibrium ideal.

This dichotomy within the same dung community concurs with Hanski's (1991) population-dynamic classification of the dung community as being governed by either resource pre-emption, lottery dynamics, which describe the ability of large beetles to dominate a resource patch, or variance-covariance dynamics where many species stay and possibly interact over an extended period. The most obvious interaction expected is competition, but its role as an organiser within this community is still a matter of debate. No single dominant force may be required to explain community formation, competition might be just one of many (Arthur, 1987), and lack of competition may be equally important (Masters and Rayner, 1993). Whatever the role of competition in the foundation of a community, it

almost certainly has had a coevolutionary "fine-tuning" effect, but this effect may be rare and subtle as there is little solid evidence for it (Southwood 1987; Connell, 1983), although this perception may be changing (e.g. McGeoch and Chown, 1997, Gotelli, 1997). So, where does one look for effects of competition? Simple systems should show competition or its results (Arthur, 1987; e.g. Young *et al.*, 1997), and presumably if interspecific competition occurs in a community, it will be most detectable in a small subset of ecologically similar species (Colwell and Winkler, 1984). That is the level at which this study is placed; in a taxonomic subunit of a guild of predatory dung dwelling beetles.

Over the years, population biology has seen recognition of the importance of historical events in the structure of communities go out of fashion, only to be embraced again as ecologists took on a more balanced view, that patterns of diversity are caused by a variety of evolutionary and ecological processes, including geographical effects and historical events (Schluter and Ricklefs, 1993). So now large-scale regional effects are compared alongside smaller local issues to explain structure and function of ecological communities.

1.2.1 Local processes

A species' presence or absence in a community depends on processes tending to increase or decrease species numbers. Local processes are seen as decreasing forces, (MacArthur, 1972; Ricklefs, 1987), through the effects of predation, disease, competition and adaptation. Some of these processes are directional, being "top-down" such as parasitism, competition or predation, or "bottom-up" in the form of resource quality and availability (Cornell and Lawton, 1992). These processes assume different importance depending on which guild or functional group (Doube, 1990), of the dung community is examined. Scarabs are strongly influenced by resource quality (Aschenborn *et al.* 1989; Cook, 1993; Emlen, 1994), and predation and parasitism appear to be slight (Cambefort, 1991).

Competition is assumed to be fierce, but mainly among the large scarabs (Heinrich and Bartholomew, 1979; Giller and Doube, 1989; Doube, 1991). Coprophagous flies seem to be squeezed from all sides, in terms of dung quality (Ridsdill-Smith, 1990), competition from dung beetles (Doube *et al.* 1988) and each other (Doube and Moola, 1987), and finally predation from other fauna (Doube and Huxham, 1987; Doube *et al.*, 1988; Hu and Frank, 1996).

Predatory beetles appear to have few of their own predators or parasites (Hanski, 1991). The dung habitat will shield them from extremes of climate and, as generalist feeders, resource availability is unlikely to be a constraining factor. If food is not limiting then there is no clear "top-down" or "bottom-up" label which can be applied to this guild. The patchiness of the dung habitat has a major effect on community processes that take place within it and one of these effects is the aggregation of species.

1.2.1.1 Aggregation

Aggregation can be either inter- or intraspecific or both, but the causes and consequences are probably similar. Aggregated distributions are the usual pattern found in insects living in patchy habitats (Ives, 1991; Kneidel, 1985; Atkinson and Shorrocks, 1981; Forsyth and Robertson, 1975) and dung beetles are no exception to this (Giller and Doube, 1994; Kohlman, 1991). Hanski (1980a) found temporal and spatial aggregation between two species of *Sphaeridium*, leading to the question of why similar species would overlap so strongly in their choice of habitat. The ecological similarity of the species may well be one of the major causes of this aggregation. The more similar two species are the greater their spatial and temporal correlation across similar resource patches is expected to be (Hanski and Cambefort, 1991a).

Heterogeneity of the resource patches and the movement behaviour of the insects may cause interspecific aggregated patterns of distribution. This seems to be unlikely in the case of dung beetles, where the patches are produced by the same species of mammal in the same place at the same time. If one of the consequences of intraspecific aggregation is to increase the likelihood of conspecific males and females meeting (den Boer, 1981), then aggregation will be advantageous. Many species of beetles do pair up on the dung pat (e.g. Sato and Hiramatsu, 1993) and pheromones have been shown to be used by at least one species of *Kheper* for long distance sexual signalling (Tribe, 1975). Pheromone glands have been found on several other species of dung beetles (Houston, 1986; Plout-Sigwalt 1982; 1986) but their precise function is unknown (Tada and Leal, 1997), and it seems more likely that they would serve as short-range signallers in the dung. Mate finding has nothing to offer as an explanation for interspecific aggregation.

As with many other dung beetle behaviours, aggregation is not an all or nothing outcome, and, as with other phenomena, the opposite ends of the gradient correspond to differences in size. Aggregation has been found to decrease with increasing size and specialisation, which also appear to be linked (Cambefort, 1991). Taxon (tribe) was found to be less important than size in its effects on interspecific distribution (Hanski and Cambefort, 1991a).

Whatever the causes of these aggregated patterns (and stochastic effects of weather have not been considered, but will obviously influence any ecological cause), the consequences of such spatial patterns are potentially great, particularly the possibility that they facilitate the coexistence of competitors. Ives (1991) has shown that aggregated interactions among competing individuals of the same species will allow coexistence of competing species with greater competition coefficients than would be possible without aggregation. Therefore intraspecific and interspecific competition are drawn together in a state of balance, where more intraspecific aggregation leads to increased intraspecific competition which allows interspecific coexistence. If aggregation mediates coexistence in this fashion, it

can be seen as comparable to coexistence based on resource partitioning, although the underlying mechanism is fundamentally different (Ives, 1988).

Exactly how much aggregation is required to allow coexistence? No magic number has been arrived at, (Atkinson and Shorrocks, 1981; Hanski, 1981; Ives and May, 1985), but assuming that intraspecific aggregation is the main determinant of guild size, Shorrocks and Rosewell (1986; 1988) have calculated between five and seven species would be able to coexist in a guild of frugivorous *Drosophila*. Recent field data from Sevenster and van Alphen (1996) lends support to this theoretical prediction. Looking at beetle distributions in dung pats, again the picture is very variable, Kohlman (1991), found extreme patterns of aggregation of a dung scarab *Ateuchus carolinae* in Mexico. However, Macqueen and Doube (unpub. in Hanski and Cambefort, 1991) found a random distribution of introduced scarabs in Australian pastures. Neither may represent a typical pattern for dung fauna, but Giller and Doube (1994) found aggregation at various scales in southern African scarabs, with beetle size again playing a significant role.

The size of individuals appears to be a pivotal issue in how we should predict behaviour of members of the dung community. Smaller, generalist species would be expected to be aggregated and exhibit variance covariance dynamics, while larger specialists should be more randomly distributed, interacting in a lottery type dynamic (Hanski and Cambefort, 1991a). With regard to staphylinid populations, what expectations are generated from the above patterns in scarab behaviour? Certainly most of the predatory species are generalist feeders (Hafez, 1939a; Hanski, 1991) and have been observed eating all manner of soft-bodied prey. They are small, obviously with a range among the subfamilies, but most importantly in relation to the habitat (pat) size. Large scarabs can dominate a pat because they are able to sequester a large proportion of it in a short space of time, clearly even the largest staphylinid is incapable of such control in a cow pat. Therefore one would predict that dung breeding staphylinids should exhibit an

aggregated distribution as part of an assemblage of small species in which intraspecific and inter specific aggregation are critical ingredients of coexistence.

1.2.1.2 Coexistence

Part of the conundrum in identifying competition is the requirement that the potential competitors coexist, doing the same thing, in the same place at the same time. This manner of coexistence is clearly impossible, but nevertheless insects have been shown to co-occur in clearly defined habitats such as swollen-thorn Acacia trees (Young *et al.*, 1997), *Heliconia* water-filled bracts (Seifert, 1984), and bracken (Lawton, 1984). However, given the complex structure of plants compared to that of a dung pat, these species could be described as co-occurring rather than coexisting and these communities are generally viewed as largely non-competitive, loosely associated guilds of species drawn together by evolutionary stochastic events (McGeoch, 1995).

Hanski (1980a) found almost perfect overlap in the distribution of two species of *Sphaeridium* (Coleoptera: Hydrophilidae), examined at scales from field down to pat. Many scarabs appear to coexist on this basis (Anderson and Coe, 1974; Holter, 1982; Hanski, 1991) and classical resource partitioning is insufficient to explain the coexistence of so many species using the same resource (Schoener, 1974). Other suggested mechanisms facilitating coexistence are parasitism or predation which are thought to exert "top-down" control in herbivore communities (McGeoch, 1995). The effect of parasites and predators on dung beetles is uncertain with few direct observations (Paschalidis, 1974; Davis, 1977; Bernon, 1981, in Doube 1991). Therefore the role of this control mechanism in the dung habitat is unknown. Resource partitioning would appear to occur between some sympatric dung scarabs which exhibit a suite of characters such as the way they handle dung, their digging ability related to soil type, and temporal variation in seasonal successional and diurnal occurrence (Doube, 1987; 1991). All of which,

in conjunction with aggregation, may lead to discontinuous competition and facilitation of coexistence in subtropical southern African savannas (Hanski and Cambefort, 1991b), which are generally seen as competitive environments. Interestingly, West African tropical savannas are seen as even more competitive, and those populations of dung rollers are thought to be coexisting under the influence of strong continuous competition (Cambefort, 1991).

1.2.1.3 Competition

Historically, ecologists have believed that competition is of prime importance in structuring communities. This idea goes back to Darwin, who suggested that competition was a driving force in evolution and dictated the presence or absence of a species in a community. Mathematical models of population dynamics by Lotka and Volterra, and Gause during the 1920s and 30s led to the principle of competitive exclusion, which held that close competitors could not coexist. Hutchinson's (1959) "Homage to Saint Rosalia" established the concept of limits to similarity, using the size of coexisting species as one dimension of many that are used to partition resources within a community. Supporting data from the field (MacArthur, 1958; Pianka, 1967), and laboratory (Park, 1962), contributed to the success of the theory and creation of more sophisticated models (May and MacArthur, 1972; Roughgarden, 1974, 1976, 1979). The late 1970s and early 1980s saw an attack on this golden calf of competition, primarily from one quarter, Florida State University and the colleagues of Daniel Simberloff, whose zealous advocation of the use of null models to test assumptions of size distributions eventually resulted in the debate descending into acrimonious rebuttals (Gilpin *et al.*, 1984) of which the highlight was that even though "Santa Rosalia" was revealed to be a goat, she nevertheless retained her mystical powers (Lewin, 1983a). These events are now generally viewed as having been useful in

getting ecologists to test their data and conclusions more rigorously against alternative hypotheses such as mimicry, hybridisation or crypsis (Arthur, 1987).

Overall, the conclusion reached is that competition does occur but it depends what community you wish to look at. For example, despite greater than 70% overlap in exploitation of plants by thirteen species of stemborers, competition was only detected between two of them in a study by Rathcke (1976). Herbivorous insect communities make up 25% of all extant species (Southwood, 1978), yet competition is rarely found, and top-down pressure from predators and parasites is the overriding force (Lawton, 1984). Apparent competition, where one species affects another mediated through the presence of a shared predator, is apparently fairly common (e.g. Müller and Godfray, 1997), but periodically disappears from the scientific consciousness (Holt and Lawton, 1994). Predator mediated apparent competition may allow coexistence in such communities. However, it has also been suggested that horizontal effects such as interspecific competition are frequent, but subtle and difficult to detect (Southwood, 1987). When the effect of natural enemies is reduced in high quality ephemeral resources such as galls, then competition between phytophages for this limited resource may be found (McGeoch and Chown, 1997).

In vertebrate assemblages, birds' bills have received most attention, particularly Darwin's finches, where the ayes have it for competition, but Wiens (1984) counters that, in his studies, niche overlap in dietary composition of individual species varied from year to year, and could therefore not be related to size differences in birds. It would seem that it all depends on which part of the ark you decide to look at (Lawton, 1984), and a broad approach should be adopted more often than narrow detailed studies.

Evidence of competition from predatory arthropods is equivocal. Spiller (1984) found interference competition between spider species A and B, and exploitation competition between species B and C. Carabids are probably one of the best

studied groups of predatory insects on the planet (Stork, 1990). den Boer (1980) could find no convincing evidence of interspecific competition in carabids, and went so far as to propose that the principle of competitive exclusion be replaced by the principle of coexistence. Niemela (1993) reviewed 32 papers on coexisting carabids, of which only half claimed that interspecific competition existed. Of those, the evidence presented was considered weak because most authors could not dismiss alternative explanations. Larval competition was neglected in most of these studies, but may be more important than adult interactions. Gotelli (1997) found two species of larval ant lions coexisting with interspecific competition, but concluded that these effects were indistinguishable from intraspecific interactions. Istock (1965) found larval cannibalism in three species of dytiscid, and used it to explain latitudinal species clines But the experimental set-up in these trials was very artificial, and food was a limited resource. Chains of competitive displacement along a geographical gradient are also open to criticism as a regional or physiological effect. Schultz and Hadley (1987) reached this conclusion from their study of physiological differences between cicindelid species, which they found to be conserved across the geographical range of the beetles.

Competition in the dung insect community is accepted as being severe, partly as an explanation for dung scarabs having evolved specialised methods (categorised as "functional groups" (Doube, 1990)) of sequestering dung, apparently as a means of monopolising a portion of this valuable resource. Telecoprids, or rollers, cut balls out of the dung and roll them away to be buried or concealed in vegetation. Paracoprids, or tunnelers, bury dung directly beneath the pat, and endocoprids, or dwellers, feed and breed in the dung pat itself (Paschalidis, 1974; Holter, 1979; Halffter and Edmonds, 1982; Davis, 1989). Diversity of nesting sites and depths is also taken as a form of spatial segregation in the Scarabaeidae (Edwards and Aschenborn, 1987; Doube, 1987; Davis, 1989). Anecdotal observations of fighting by telecoprids may contribute to this impression of a very competitive habitat. However, Heinrich and Bartholomew (1979) have provided elegant experimental evidence of competitive behaviour linked to physiological

adaptations in telecoprids. Nevertheless, it is intriguing why beetles still fight at times when there is ample dung and few competitors. As to the other functional groups, competition is assumed amongst paracoprids (Hanski and Cambefort, 1991c) and demonstrated as asymmetrical by Giller and Doube (1989). Beetles compete for space beneath the pat (Bernon, 1981, in Hanski and Cambefort, 1991c), and may be subject to interference competition in the pats, which causes increased emigration from pats by *Aphodius* as density increases and oviposition rates fall (Holter, 1979; Yasuda, 1987).

As with many features of the dung scarab community, there is an apparent hierarchy of competitiveness, from assemblages dominated by telecoprids and paracoprids at low latitudes, to endocoprid dominated temperate communities. Diel activity may separate fast tunnelers and rollers, but small tunnelers and slow burying tunnelers will interact with pat dwelling species (Hanski and Cambefort, 1991c). This is where competition should be most severe as both adults and larvae are tied to the pat for feeding, breeding and development. However, Holter (1982) has not found any competitive effects within the *Aphodius* species. Staphylinids will be at this end of the hierarchy and will be tied in the same way to the resource, as are *Sphaeridium* species which overlap extensively in habitat use, but show no signs of competition (Hanski, 1980a).

In what sort of community would one expect to find competition? Given that coexistence is a reality within all communities, then in principle, competition should be strongest in communities in moderately harsh environments. Those in benign habitats will be controlled by parasites and predators, while harsh conditions will depress populations below the level at which they will compete (Connell, 1980). This creates some difficulty in classifying the habitat, as dung pats in many respects appear harsh in that they are short-lived and prone to complete destruction, yet they are resource rich and ameliorate the extremes of temperature and humidity of the surrounding pastures. Maybe they are moderately harsh, but this classification is shaky because a habitat surely is not harsh if you

are adapted to live in it. The next question arises, is the dung community near or at equilibrium, or closer to non-equilibrium? Using Wien's (1984) categories, the scarab fauna would tend towards the equilibrium end of the scale, appearing to be resource limited (at times), influenced by close biotic interactions, and subject to competition (Giller and Doube, 1989; Hanski and Cambefort, 1991c). What of the predatory guild? They are small, likely to follow a variance-covariance dynamic and be susceptible to large stochastic effects. One would predict that they will be closer to a non-equilibrium categorisation and be resource limited, but prey are always available for these generalist feeders and habitat patches are often unoccupied. Unfortunately, resource limitation is one of the key requirements for competition to occur (Connell, 1980) and is unlikely to be found in populations of dung staphylinids. It is difficult in general to find natural populations that are limited by their food (Arthur, 1987), just as niche overlap is a very common natural state of affairs - species are not clearly segregated. So, in looking for mechanisms of coexistence of sympatric species, resource limitation of food is assumed to not exist, therefore other parameters should be examined, and the extent of niche overlap investigated to look for the effects of competition or coevolution caused by competition.

1.2.1.3.1 Measures of Competition

Although resource overlap does not measure the amount of competition between species it can be used either as evidence for or against competition between species (Colwell and Futuyma, 1971). The two techniques most commonly employed involve, either looking for the "ghost of competition past" (Connell, 1980), in the shape of (usually), morphological changes which constitute character displacement (Schluter, 1994), or experimentally manipulating a community, typically by the removal or addition of a species (Wise, 1981), and looking for the expansion or compression of niches. Each method has its shortcomings. The

natural situation needs a control sample which requires a matching habitat that differs in only one major factor, which clearly does not exist, and perturbation experiments are too short term to see anything other than phenotypic effects (Lewin, 1983b). So, rather than using direct observations of competition which, in most situations, is regarded as having been evolved away, the outcomes of competition are used to determine its presence

Extinction of one species by a competitor has been achieved in laboratory colonies, although this does have alternative explanations of temperature adaptation in *Drosophila* (Arthur, 1987) and inconsistent outcomes in *Tribolium* (Park, 1962). The reverse experiment of looking at establishment of introduced species into new habitats has too many other potential plausible reasons, such as unsuitable habitat for failures, and empty niches for successes. The effect of introduced dung beetles on native species is considered to be negative (Howden and Scholtz, 1985), though given the fluctuation in natural populations recorded by Doube (1987), this could represent normal cycling of the population.

There is general agreement that morphological adaptations are evolutionary responses to ecological conditions (James and Boecklen, 1984). The next step in the logic is to attribute these adaptations to resource partitioning, which can take the form of differences in foraging efficiency (Hanski and Ranta, 1983; Schluter, 1994), but is most commonly seen as well spaced out body sizes resulting from limits to similarity (Hanski and Cambefort, 1991b). How well spaced out these sizes should be is where Hutchinsonian ratios are invoked (Hutchinson, 1959). May and MacArthur (1972) argue that very small differences in the ecology of two species may not be enough to allow stable coexistence.

In conclusion, competition, if it exists in the system in question (dung dwelling *Philonthus*), is likely to be difficult to detect, and will be influenced by other factors such as aggregation and covariance of species. The size of the beetles relative to dung pat, and the assumption that *Philonthus* are generalist predators

should both reduce the likelihood of competition. Therefore, it appears that competition itself is unlikely to be seen, and it should prove more fruitful to look for the evolutionary outcomes of competition, if they exist, between three species of co-occurring *Spanlonthus*.

1.2.2 Regional Effects

Interspecific interactions may be important at a local level, but are not a satisfactory explanation of differences between communities at a regional level simply because adaptations that are found in sympatry generally extend throughout the allopatric species range. Presumably, this glaring fact has been one major reason for reintroducing large scale regional issues back into ecology, and the recent attempts at integrating traditional subjects such as "a revitalised natural history", palaeontology, systematics and biogeography (Schluter and Ricklefs, 1993). It is now accepted that biogeographic factors influence community structure rather than intrinsic local processes, so that regional species richness is freed from local constraints. Therefore, control is from regional to local and is therefore extrinsic (Cornell and Lawton, 1992). The two major regional effects on communities are climatic and historical (how, where, why speciation has taken place).

The distribution of most organisms, but particularly insects, is closely linked to climate (Uvarov, 1931); with strong patterns associated with latitudinal gradient (Menge and Olsen, 1990; Tilman and Pacala, 1993). Many competitive explanations for displacement are better explained as regional responses to climate (e.g. Istock, 1967). Dung beetle communities at higher latitudes are characterised by the dominance of *Aphodius* species and the absence of large telecoprids (Hanski and Cambefort, 1991d). This situation is almost reversed at tropical latitudes where telecoprids and large tunnelers predominate. It is tempting to speculate that this could be driven by some physiological constraint on performing

energetic behaviours at lower ambient temperatures. Interestingly, in the subtropical regions *Aphodius* does not disappear (there are many species in South Africa), but shift their seasonal activity to drier periods when the other guilds of scarabs are not active (Davis *et al.* 1988). Of note is the similarity between numbers of local assemblages of dung-dwelling staphylinid species in Europe and in Africa. The slight decrease in numbers in South Africa is attributed to an effect of the scarab fauna dominating the dung resource, removing the flies which are preyed upon by staphylinids (Hanski and Cambefort, 1991d). It seems more likely that the African staphylinid fauna is less well-known than its European and American counterparts (Smetana, 1995).

Climate seasonality, seen as changes in temperature and rainfall largely determine insect activity times (Wolda, 1988). This effect is particularly marked in dung beetles, many of which are dependent on rain softened soil in which to bury dung (Davis, 1995). This effect may be not so marked in those species, such as staphylinids, that can complete their life cycle in the pat and drainage zone below it. Different life history strategies are seen as adaptations to seasonality in species that have other similar ecological requirements (Wolda, 1987).

Climate therefore has an overall influence on the occurrence and abundance of species tolerant to a particular set of climatic conditions. These have either a direct effect on population abundance, or an indirect effect via biotic interactions such as competition or predation. Fixed traits in physiology that are found across the geographic range of an insect (Schultz and Hadley, 1987) are a contradiction to the assumption that animals are adapted to local climate, although some of these effects may be confused by phenotypic plasticity. Once again the alternative hypothesis must be considered, that allopatric speciation followed by range expansion, brought together by chance an assemblage of individual species with similar ecological requirements, and that any differences between the species are part of their history, fine tuned by adaptation and not mechanisms of coexistence. Jay-Robert *et al.*, (1997) concluded that history has dictated the origin and

composition of dung beetle assemblages in the Sierra Nevada and Central Iberian mountains of Europe, in contrast to their findings for the fauna of the European Alps, which they judged to be influenced by local processes at the community level. Kohlman (1991), looking at forest dung beetles in different biomes, concluded that the assemblages look very similar despite their clearly different phylogenetic origins of either North American or South American invaders.

These issues of scale are of particular interest in the current anthropogenic extinction episode. Nee and May (1997) have recently calculated that 80% of evolutionary history will survive a 95% loss of species. In contrast, Hughes *et al.*, (1997) compute that 1800 populations per hour are being exterminated in tropical forests, the "powerhouses of global evolution". Looking at communities from the larger regional scale, to the smaller local scale, it is evident that local processes such as competition, predation, exclusion and stochastic variation contribute to local species extinction, in the face of regional processes of species formation and geographic dispersal (Arthur, 1987).

1.3 Evolution of Communities

The assumption of discrete allopatric speciation leading to chance formation of communities bears some examination. Schluter (1994) has convincingly demonstrated rapid character displacement in response to interspecific competition. Nevertheless, his results can be explained as local adaptation in a species' phenotype. We do not have the resources or time to watch establishment and dispersal of a new species in existing communities. If adaptation and species packing has already taken place, then establishment of a novelty should not be possible. The successful introduction, deliberate or otherwise, of exotic species into new habitats refutes this idea. Unsaturated communities are ubiquitous (Cornell and Lawton, 1992), theoretically part way in the race between the

widening phenotype of the first species and dispersion to the new habitat by other ecologically differentiated species (Roughgarden, 1972).

The most important question therefore is do unused resources allow ecological release (MacArthur and Wilson, 1967)? The process would be expected to be slow, during which time competition will be intermittent and inconsistent. Most species are considered resistant to change, as they are evolved for syngamy at least as much as they are adapted to their environment (Gould, 1982; Paterson, 1985). Convergence then is better interpreted as evidence of constraints of the environment rather than evidence of pre-existing niches (Masters and Rayner, 1993).

Walter *et al.* (1984) feel that the concept of an organised community is unrealistic and that communities are not adaptive devices. Because the geographical ranges of any two species are unlikely to coincide exactly, competition must be a local phenomenon. Benton (1987) dismisses the role of competition further, by concluding that the fossil record demonstrates that extinction and replacement events can be linked to mass extinctions, rather than evolutionary progress and improvement in competitive abilities. So, it is concluded that lack of competition is associated with major evolutionary change (Arthur, 1987), as animals are envisioned radiating out into this new and unclaimed empty niche space. But, as has been noted, most species resist evolving. Therefore in the face of environmental change, they will track tolerable environments across continents - "the ability to evolve out of trouble is beyond the genetic agility of most species" (Coope, 1979). The major influence from the environment is in all cases temperature (Masters and Rayner, 1993). So we end up with the conclusion that habitat destruction, not ecological space is the main force behind evolutionary change. "Presence or absence of other species with similar ecological requirements is irrelevant to the generation of novelties" (Masters and Rayner, 1993). Consequently, the "hotel of resources" does not have every room filled

because, either the prospective occupants have not yet arrived, or no suitable occupants exist (Rohde, 1997; Price, 1984).

1.4 Value of the *Spatulonthus* system.

Why choose this particular subset of the dung-insect community to look for evidence of coexistence and coevolution? The answer is partly historical, in that it was the community best known to me, and that it is interesting because it is little studied despite the biocontrol potential of its members. In addition, dung is a habitat that has great potential for ecological studies. Observations on any vagile organism require decisions on where and when to sample (Levin, 1992), and most communities have a spatially open structure where species may extend into other communities (Schluter and Rickleffs, 1993). The dung pat overcomes these problems by being a strictly defined habitat in time and space, which is easy to manipulate and to recreate in the laboratory. The coprophagous scarabs have been fairly well studied and excellently reviewed recently (Hanski and Cambefort, 1991c). Therefore, because the staphylinid fauna of dung are relatively unstudied (Davis *et al.* 1988; Davis, 1996a), and dung scarabs are assumed to be similarly affected by shared biotic and abiotic influences, the scarabs are used throughout this study to review current thinking on the topics covered, and to predict what might be expected of the experimental animals. The subgenus *Spatulonthus* forms a closely related subgroup of a few species, within a large dimensional system which should be ideal for observing the results of coevolution (Connell, 1980), although from the above review, the chances of seeing competition in action are poor. Nevertheless, predators using a patchily distributed resource should be aggregated (Keddy, 1989), and if the competition is or was potent enough, some evidence of it should still be manifest - "the ghost should still be found" (Lawton, 1984).

1.5 Aims of this research

The aim of this study was to look for coexistence in three members of the subgenus *Spatulonthus*, and for adaptations that facilitate that coexistence. From these data, generalities are explored by drawing conclusions about the origins of the adaptations studied.

The first chapter introduces the topic of coexistence. The biology of dung staphylinids with an identification key is discussed in Chapter 2. Field sites and methods are also covered. Mating behaviours of the three *Spatulonthus* species are used in Chapter 3 to confirm their specific status. Chapter 4 examines coexistence between the species at different spatial and temporal scales. Chapter 5 relates the beetle's distributions to thermal biology of the species. Life history traits are compared in Chapter 6, and evidence of character displacement and competition are dealt with in Chapter 7. Chapter 8 serves as a conclusion to the study.

CHAPTER TWO

FIELD SITES AND STUDY ANIMALS

2.1 Introduction

2.1.1 The Dung Fauna

Of the animals utilising the dung habitat, Diptera and Coleoptera are by far the most successful. Adult Diptera are visitors to dung pats to feed, mate and oviposit, but their larvae develop in the dung and are mainly coprophagous, (Muscidae, Sepsidae, Sphaeroceridae and Scatophagidae). They eat the liquid portion of the dung and consequently are early arrivals at droppings. Some species of Muscidae are predatory (Hanski, 1991). The Coleoptera are represented by four main families of which the Scarabaeidae are exclusively coprophagous and the Histeridae are predacious. The Hydrophilidae are coprophagous as adults, with predatory larvae, and the Staphylinidae have a variety of lifestyles including coprophagous Oxytelinae, predatory Staphylininae, and the Aleocharinae, of which most dung-dwelling species are predatory as adults, and some are dipteran pupal parasitoids as larvae.

2.1.1.1 The Staphylinidae

The family Staphylinidae is one of the largest and most successful families of beetles with at least 1500 genera and well over 30,000 species world wide (Smetana, 1985). The southern African Staphylinidae are poorly known, with about 150 genera and 750 species recorded to date. The family was treated for southern Africa by Scheerpeltz (1973), and Smetana (1985) gives a key to the major South African subfamilies. The taxonomy of the group, particularly the Afrotropical fauna, is in disarray and many revisions are long overdue (Smetana, 1995). The size of the

genera and the way in which many descriptions have been published make the task a daunting one. Boheman in the 1840s and Bernhauer in the 1930s were responsible for much of the early work in Africa. Tottenham (1949a,b; 1953; 1955; 1956; 1957; 1962) and later Levasseur (1962; 1969; 1971; 1980) have followed up this work, but as a consequence, most of the type specimens lie in European collections. Many species have been described several times over (P. Hammond, pers. comm.) and many old world species are turning out to have a cosmopolitan distribution (Frank 1983), either as indigenous species or accidental introductions (Sm[illegible], 1995).

The genus *Philonthus* Stephens contains over 1000 species, but recent cladistic analysis does not support the monophyly of the group which needs to be resolved (Smetana, 1995). *P. sanamus* was originally described as *P. nitidicollis* by Klug 1855 from a single female. The name however was preoccupied by *nitidicollis* Lacordaire 1835. Tottenham (1955) proposed a new name for it, *P. sanamus*, and at the same time, erected a new subgenus, *Spatulonthus*, of which *P. incognitus*, *P. labdanus* and *P. sanamus* are the largest members in South Africa. The species of *Spatulonthus* are characterised [illegible]nale genitalia, which have the median lobe flattened, broad and rounded at the apex. There is a single paramere situated asymmetrically on the right side of the median lobe, when viewed with the proximal opening uppermost. The position of the aedeagus at rest in the abdomen is considered diagnostic, even though it may be different in some species within one genus, including *Philonthus* (Smetana, 1995). In *P. incognitus*, *P. labdanus* and *P. sanamus* the aedeagus is generally found with the proximal opening and paramere facing dorsally, although this was found to vary between individuals. In addition to *P. incognitus*, *P. labdanus* and *P. sanamus*, there are three other species of *Spatulonthus* commonly found in cattle dung in South Africa; *P. peregrinus* Fauvel, *P. caffer* Boheman, and *P. minutus* Boheman.

2.2 Methods

2.2.1 Field Sites

Three field sites were chosen, to sample across a habitat temperature gradient from Johannesburg to Boekenhoutskloof, 100 km to the Northeast. Measuring instruments could not be left in the field at any of these sites, and local weather data were not available. Nevertheless, daily weather reports of the South African Weather Bureau gives a two degrees Celsius difference between the Johannesburg and Pretoria maximum temperatures. This is expected to represent the minimum difference between the two most widely separated sites. Davis (1996a; Davis *et al.* 1988) found no effect of soil type on *Philonthus* distribution, and all sites in this study were found to have a very similar soil type, so it is assumed that temperature dissimilarities were the main cause of differences between sites. Measuring rainfall across such a wide area would have been impractical, and it is assumed that rainfall does not have a dramatic effect on *Philonthus* activity because the adults are solely active in the dung pat and larvae tunnel in the drainage region of the soil beneath the pat.

The location of each field site was determined with a Panasonic KX G550, GPS. Altitude was measured using an altimeter (Smiths). Soil type was determined by particle size distribution. Innisfree Farm (26°06'08'' S, 28°04'31'' E; 1520m altitude; sandy loam soil type), is the southernmost, highest and presumably coldest site. Cluny Farm (25°57'09'' S, 28°03'57'' E; 1425m altitude; sandy loam soil type), is intermediate in all respects, and Boekenhoutskloof Farm (25°32'58'' S, 28°27'13'' E; 1200m altitude; sandy loam soil type), to the North is lower and presumably warmer than the other two sites.. Each farm kept a small herd of 20 - 30 dairy cows, which were pastured in various parts of the farms during the day and allowed to graze on whatever food was available. Each night the cattle were returned to the same camp, where they were watered and fed on hay, dried lucerne

and small quantities of pelleted supplements. Dung was collected in and around the camp from open positions exposed to full sunlight.

2.2.2 Identification

Identification of specimens was made with reference to the collection compiled by E. F. Davis at the CSIRO Dung Beetle Research Unit (DBRU), and identified with the assistance of Dr Peter Hammond at the Natural History Museum, London. My identifications were later confirmed by Dr Ales Smetana of Biosystematics Research, Agriculture, Canada. Using this material, a key was constructed to separate the three species under study from the 15 other species of *Philonthus* commonly found on the South African highveld. This key uses characters that can be seen on live specimens, narcotised and viewed under a dissecting microscope. Voucher specimens are lodged at the Transvaal Museum, Pretoria.

The chaetotaxy of the thorax usess the dorsal rows of punctures on the middle portion of the pronotal disc. The method used in this key is one of two commonly employed to separate *Philonthus* species (Smetana, 1995). The punctures in one of the two medial, longitudinal rows on the pronotal disc are counted. The first puncture, closest to the anterior margin of the pronotum, is not considered to be homologous with the genuine punctures of the dorsal rows and is therefore separate from the rest (Smetana, 1995), so that the total is given as a combined figure, e.g. 1 + 4, for a species such as *P. sanamus*.

2.2.2.1 Key to the genera of dung-dwelling Staphylininae commonly found on the South African Highveld.

1. Pronotum wi[illegible]two distinct, longitudinal medial rows of punctures (e.g. Fig. 1b) 2

- Pronotum without two distinct, longitudinal medial rows of punctures. Closely covered with hair and coarse punctures .....*Platydracus* Thomson

2. Punctations on pronotum 1 + 5 .....*Gabrius* Stephens

- Punctations on pronotum 1 + 1, 1 + 3 or 1 + 4 3

3. Punctations on pronotum 1 + 1 or 1 + 3 .....*Philonthus* Stephens (in part)

- Punctations on pronotum 1 + 4 4

4. Last segment of labial palpus narrower than p[illegible]nate segment. Distance between posterior margin of eye and p[illegible]terior angle of head greater than length of eye. Body length ± 5 mm ...*Gabronthus* Tottenham

- Last segment of labial palpus spindle shaped. Distance between posterior margin of eye and posterior angle of head ± length of eye. Body length >5 mm .....*Philonthus* Stephens

2.2.2.2 Key to species of dung-dwelling *Philonthus* commonly found on the South African Highveld.

1. Pronotum with 1 + 1 pairs of discal punctations (Fig. 1a). Body brown with distinct yellow stripe down e[illegible]ral suture, (aedeagus, Fig.1b) ....*P. reinecki* Schubert

- Pronotum with more than 1 + 1 discal punctations (e.g. Fig. 1c). Body brown or black, elytral suture coloured or not 2

2. Pronotum with 1 + 2 pairs of discal punctations (Fig. 2a). Body brown; faint brown stripe down elytral suture, (aedeagus, Fig.2b) .... *P. sp. nr reimecki*

\- Pronotum with more than 1 + 2 pairs of discal punctations (e.g. Fig. 2c). Body brown or black with elytral suture coloured or not 3

3. Pronotum with 1 + 3 pairs of discal punctations (e.g. Fig. 3a) 4

\- Pronotum with 1 + 4 pairs of discal punctations (e.g. Fig. 3b) 11

4. Beetle very small < 5 mm. Antennae dark, head and pronotum black, elytra black with light borders, narrow and tapering. Scutellum with fine microsculpture of transverse waves, hairs and punctations as figured (Fig. 4a, aedeagus, Fig.4b) ..... *P. nairobiensis* Fauvel

\- Beetle medium to large > 6 mm. Elytral suture may be light or dark, scutellum without transverse waves 5

5. Beetle medium to large, 7 mm - 10 mm, usually brownish in colour. Elytral suture with pale coloured stripe (e.g. Fig. 5a) 6

\- Beetle large, 10 mm +, black in colour. Elytral suture without coloured stripe 8

6. Elytra with anterior, lateral light-coloured patches on the shoulders (Fig. 5a). Mesosternal process produced into a definite point apically (Fig. 6a). Fore tarsi not dilated (aedeagus, Fig.6b) .....*P. marginipennis* Wollaston

\- Elytra without anterior, lateral light-coloured patches (e.g. Fig. 6c). Mesosternum forming a blunt process apically at the most (e.g. 6d) 7

7. Elytral suture with a very pale stripe extending posteriorally from the sides of the scutellum, and continued along posterior margin of elytra, but not leaving the margin (Fig. 6c). Mesosternum rounded apically (Fig. 6d; aedeagus, Fig. 7a) .... *P. cinctus* Fauvel

- Elytral suture with dark stripe, extending from the tip of the scutellum and continued paler along posterior margin, leaving the margin laterally to form a pale corner on the elytra (Fig. 7b). Mesosternal process forming a blunt point (Fig. 7c), (aedeagus, Fig. 7d) ..... *P. parvicornis* Fauvel

8. Beetle piceous black. Elytra sparsely covered in hairs and coarse punctations (Fig. 8a). Mesosternal process appears only as a slight ridge (Fig. 8b; aedeagus, Fig. 8c) .....*P. pseudabyssinicus* Tottenham

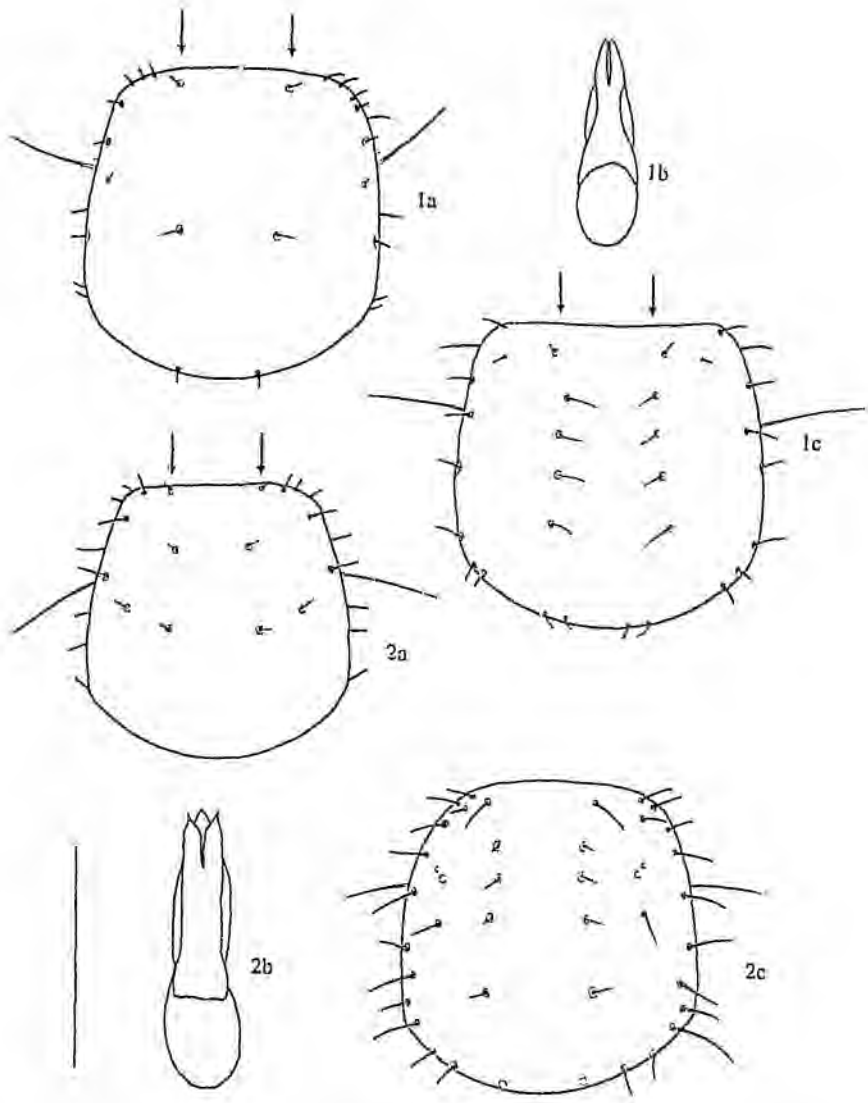
- Beetle with brown, or yellow on legs or antennae. Elytra closely covered in hairs and punctations (e.g. Fig. 8d). Mesosternal process either completely absent or forming a definite point apically (e.g. Fig. 8e) 9

9. Beetle long and slender, head narrow with elongated eyes (Fig. 9a). Elytra closely covered with smooth, fine hairs and punctations. Mesosternal process pointed apically (Fig. 8e). Abdomen shiny, sparsely covered in short fine hairs. Legs brownish. (aedeagus, Fig. 9b) ....*P. aethiops* Bernhauer

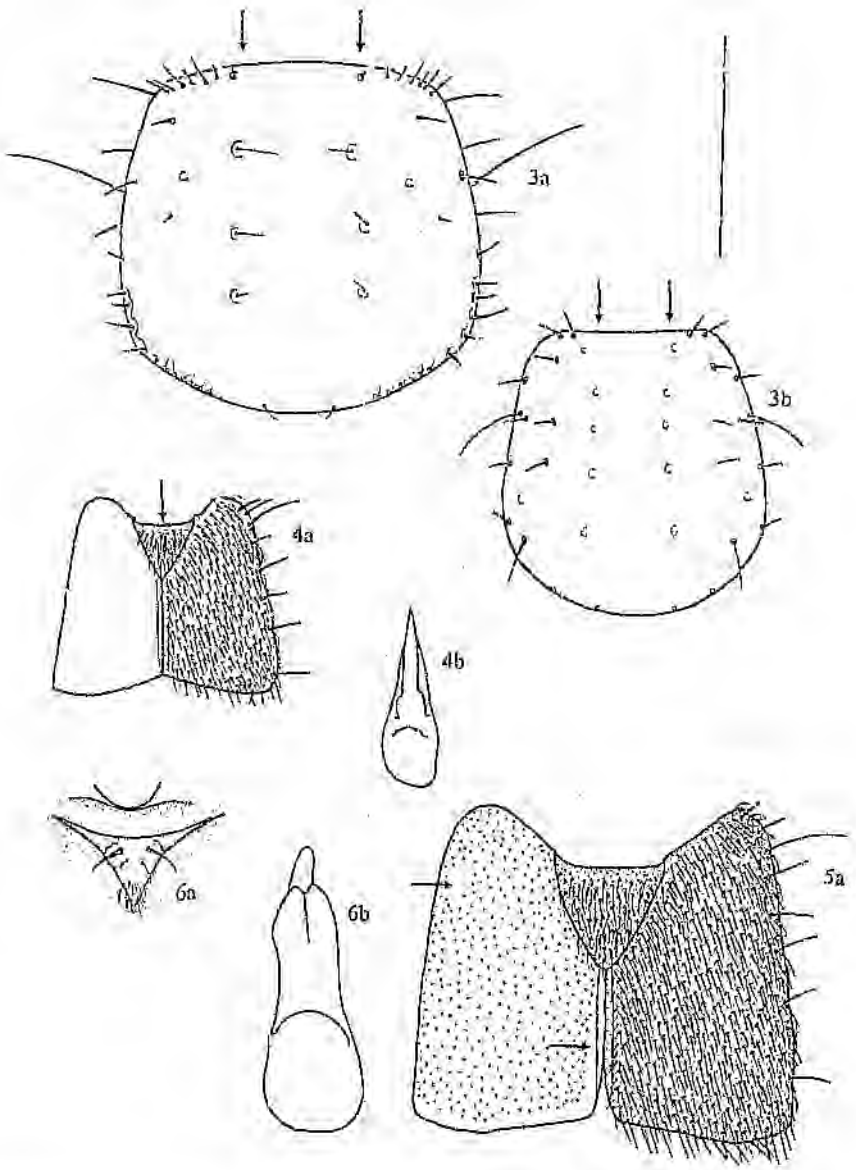
- Beetle stout, hairy appearance, head broad (Fig. 9c). Elytra densely covered in unruly hairs. Mesosternal process completely absent, only suture present (Fig. 9d). Abdomen well covered in hairs 10

10. Antennal articles all black. (aedeagus, Fig. 10a) ....*P. natalensis* Boheman

- Proximal antennal articles yellow, with last few distal articles black (aedeagus, Fig. 10a) .....*P. natalensis* var.



Figures 1-2. Pronotums and aedeagi of *Philonthus Spp.* illustrating discal punctations. The anterior edge of the pronotum is orientated towards the top of the picture in all cases. 1a, 1 + 1 punctations of *P. reinecki*. 1b, aedeagus of *P.reinecki*. 1c, more than 1 + 1 punctations, e.g. *P. sanctus*. 2a, 1 + 2 punctations of *P. nr. reinecki*. 2b, aedeagus of *P. nr. reinecki*. 2c, more than 1 + 2 punctations, e.g. *P. labdanus*. Scale bar = 1 mm.



Figures 3-6. Pronotums, elytra, mesosternum and aedeagi of *Philonthus Spp.* 3a, 1 + 3 punctation, e.g. *P. cinctus*. 3b, 1 + 4 punctations, e.g. *P. incognitus*. 4a, elytra and scutellum of *P. nairobiensis*. 4b, aedeagus of *P. nairobiensis*. 5a, pale elytral stripe, e.g. *P. marginipennis*, and shoulder patches of *P. marginipennis*. 6a, mesosternal process of *P. marginipennis*. 6b, aedeagus of *P. marginipennis*. Scale bar = 1 mm.

11. Elytral suture light (e.g. Figs. 11a, or 7a), or with a narrow pale stripe extending from scutellum to posterior margin 18

\- Elytral suture dark without a pale stripe extending from scutellum to posterior margin (e.g. Fig. 11b) of elytra 12

12. Elytral surface not completely dark, with some light areas (e.g.Fig. 11b) 13

\- Elytral surface uniformly dark, usually black or brown, with no light areas 14

13. Posterior lateral corners of elytra with distinct pale areas (Fig. 11b), usually yellow or copper coloured. Beetle medium size and slender with oval head (Fig. 13a; aedeagus, Fig.13b) .....*P. bisignatus* Boheman

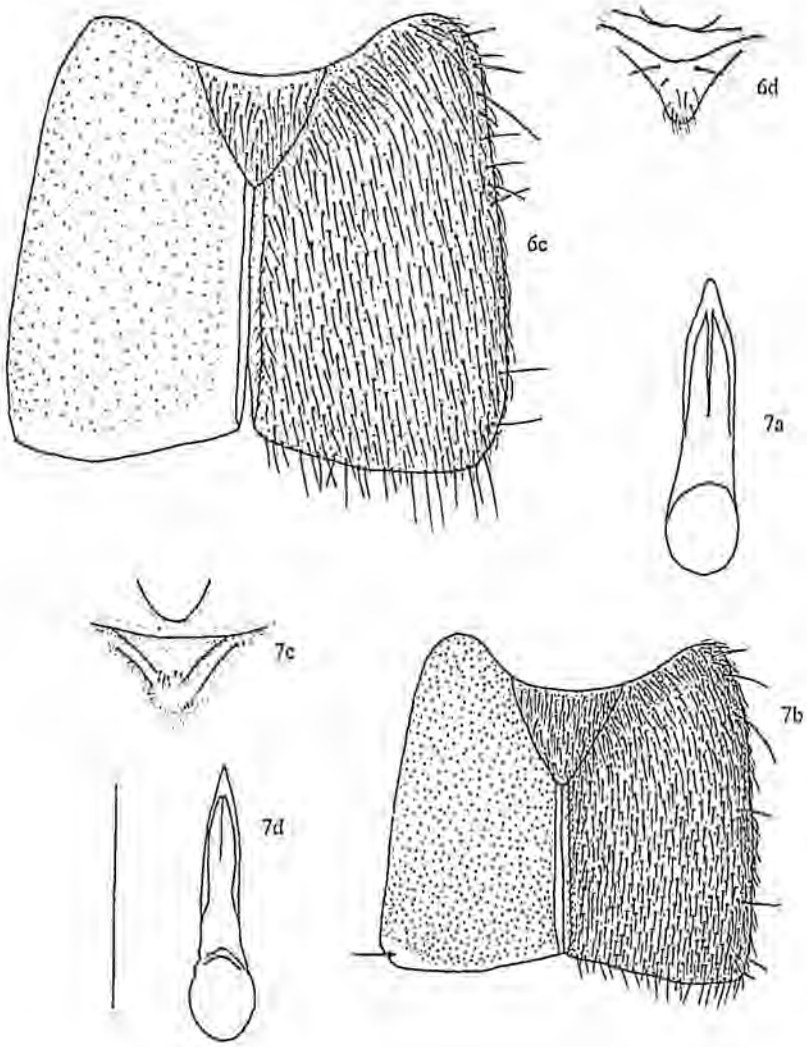
\- Elytra totally dark except for faint brown line along posterior margin (e.g. Fig. 13c). Often extending anteriorly along elytral suture as a dark line. Head broad and square (e.g. Fig. 13d) 20

14 Head-shape square (e.g. Fig. 13d). Ventral surface of fore coxae with fine hairs, no spines (e.g. Fig. 14a) 15

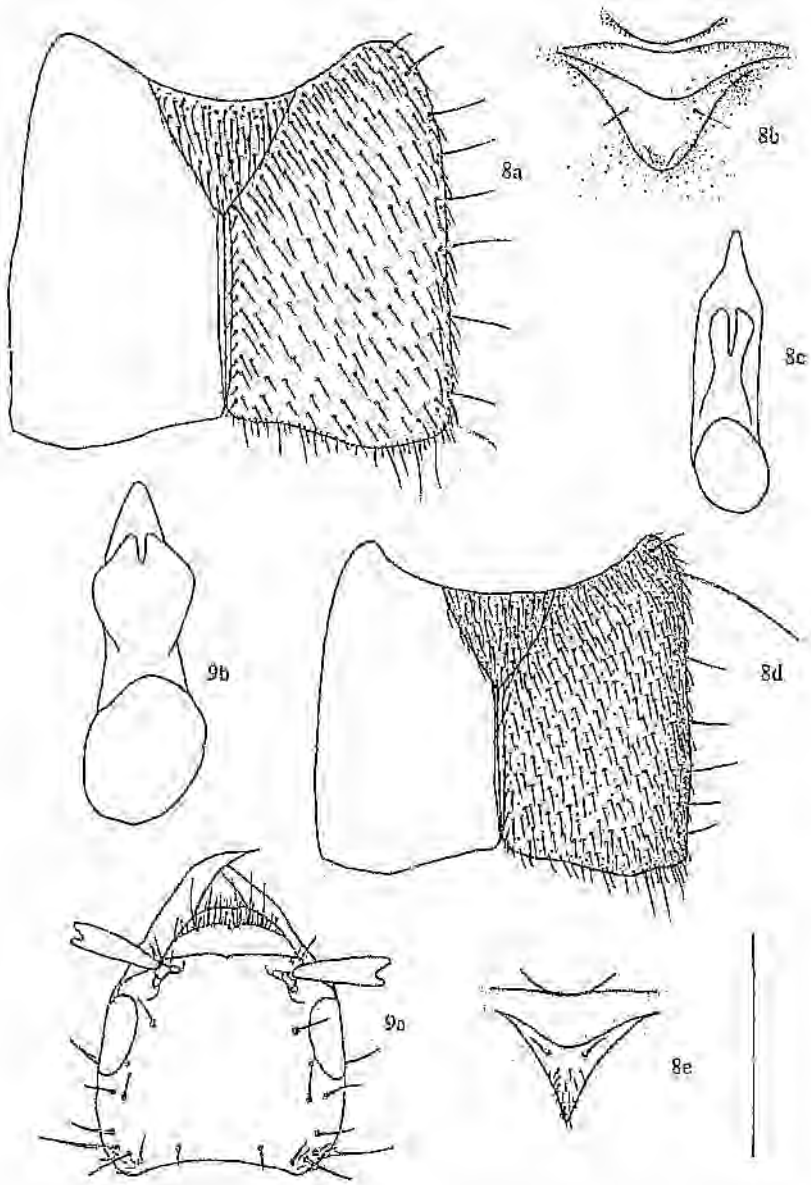
\- Head shape oval (e.g. Fig. 14b). Ventral surface of fore coxae with strong spines (e.g. Fig. 14c) 16

15. Beetle medium to large ± 8 mm. Head black, body brownish, eyes small, head broad, but not angular (Fig. 13d). Fore-tarsi not dilated (aedeagus, Fig. 15 a) .....*P. ventralis* Gravenhorst

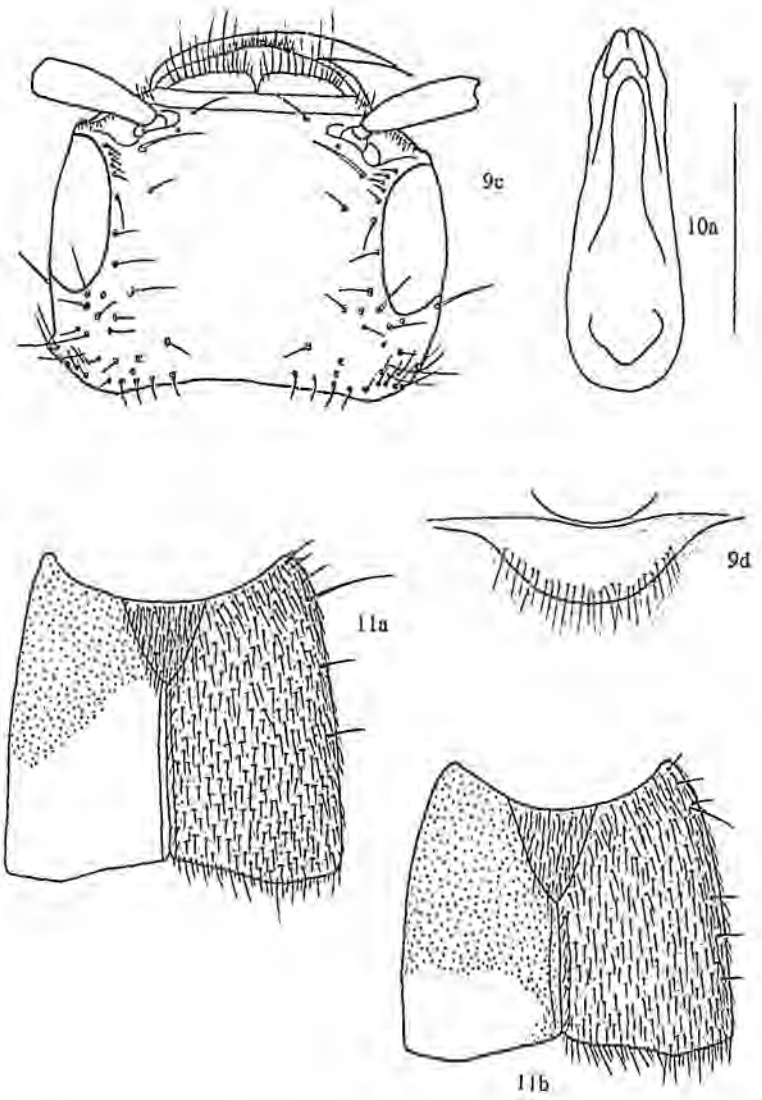
\- Beetle large, ± 11 mm. Body piceous black in colour, legs brown. Eyes large, head angular in shape (Fig. 15b). Fore-tarsi dilated (aedeagus, Fig, 15 c) ....*P. morio* Boheman



Figures 6-7. Elytra, mesosternums and aedeagi of *Philonthus Spp.* 6c, absence of shoulder patches, e.g. *P.cinctus*. 6d, blunt mesosternal process, e.g. *P.cinctus*. 7a, aedeagus of *P. cinctus*. 7b, pale lateral, posterior corner on elytra of *P. parvicornis*. 7c, mesosternum of *P. parvicornis*. 7d, aedeagus of *P. parvicornis*. Scale bar = 1 mm.



Figures 8-9. Elytra, mesosternums, head and aedeagi of *Philonthus Spp.* 8a, elytra of *P. pseudabyssinicus*. 8b, mesosternal process of *P. pseudabyssinicus*. 8c, aedeagus of *P. pseudabyssinicus*. 8d, elytra with dense hairs and punctations, e.g. *P. aethiops*. 8e, pointed mesosternal process, e.g. *P. aethiops*. 9a, head of *P. aethiops*. 9b, aedeagus of *P aethiops*. Scale bar = 1 mm.



Figures 9-11. Elytra, head, mesosternum and aedeagi of *Philonthus Spp.* 9c, head of *P. natalensis*, 9d, mesosternum of *P. natalensis*. 10a, aedeagus of *P. natalensis*. 11a, pale elytral suture, e.g. *P. caffer*. 11b, dark elytral suture, e.g. *P. bisignatus*. Scale bar = 1 mm.

16. Beetle medium size ± 8 mm. Very slender, shiny black in appearance. Elytra shiny with evenly spaced hairs and punctations (Fig. 16a). Fore coxae with dark outer surface and dark spines (Fig. 14c). (aedeagus, Fig. 16b) .....*P. peregrinus* Fauvel

\- Beetle medium to large 8 - 11 mm. Elytra closely covered in fine hairs (Fig. 16c). Ventral fore coxae with either dark or light outer surface and dark spines (e.g. Fig. 16d) 17

17 Beetle large (10 mm), fore coxae with dark outer surface (Fig. 16d), (aedeagus, Fig. 17a) .....*P. labdanus* Tottenham

\- Beetle medium (8 mm). Head oval. Body slender and hairy, with dark spines. Fore coxae completely dark. (Fig. 17b; aedeagus, Fig. 17c) .....*P. incognitus* Bernhauer

18. Beetle medium sized, ± 8 mm, and shiny. Elytra with a large pale area, usually copper-coloured, covering more than half of the posterior part of the elytra (Fig. 11a; aedeagus, Fig. 18a) .....*P. caffer* Boheman.

\- Elytral surface without large pale area, colour normally restricted to margins of the elytra (e.g. Fig. 13c) 19

19 Elytra closely covered in coarse hairs and punctations. Light stripe on elytral suture does not extend anteriorly beyond the tip of the scutellum (e.g. Fig. 13c). Fore coxae with strong dark spines (e.g. Fig. 16d) 20

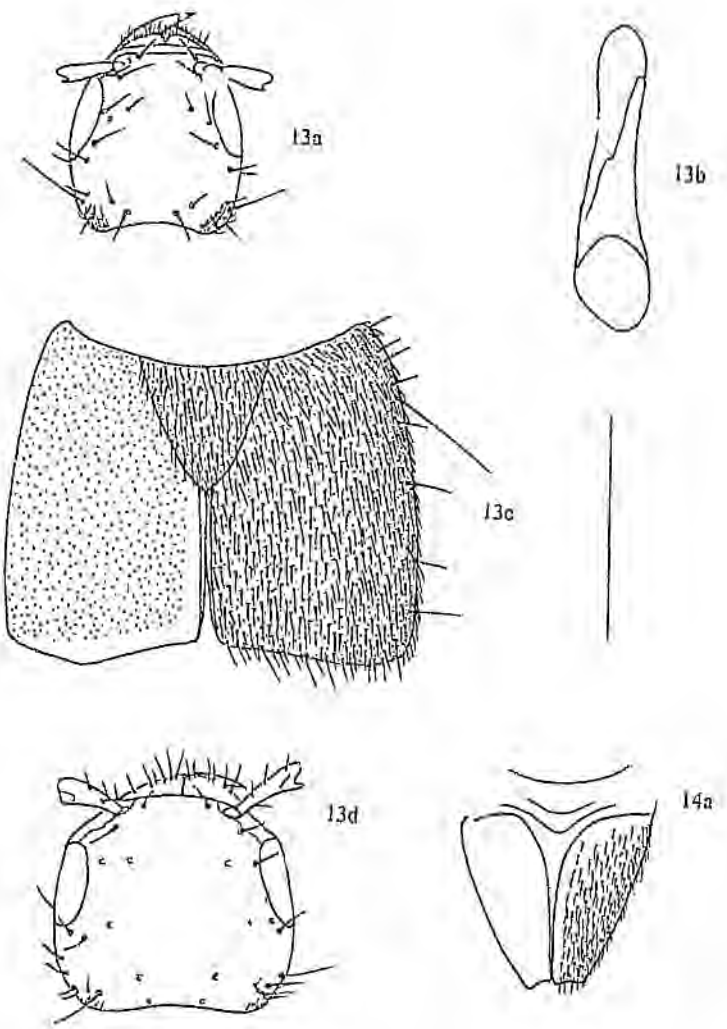
\- Elytra covered with fine light hairs. Light stripe on elytral suture extends anteriorly beyond the tip of the scutellum (Fig. 19a). Fore coxae without spines. Beetle medium to large brownish/black in colour, head and pronotum black, legs pale yellow/brown in colour, (aedeagus, Fig. 19b) .....*P. densecaudatus* Bernhauer

20. Discal punctations on pronotal disc evenly spaced, no two being obviously closer together (e.g. Fig. 3b) 21

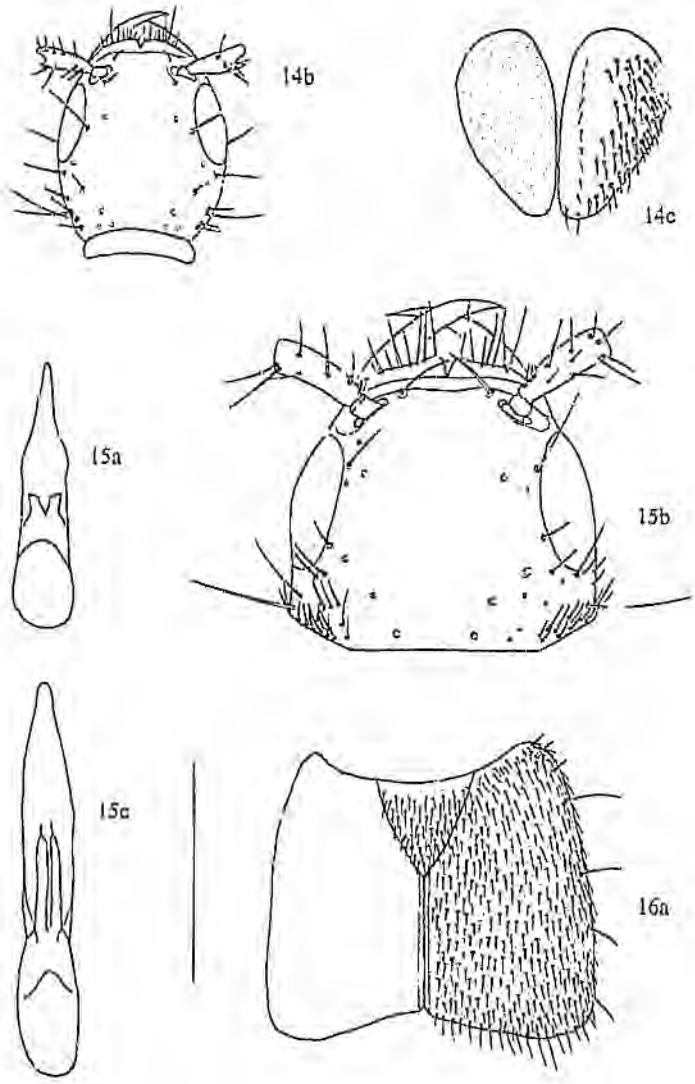
- Second and third discal punctations on pronotal disc obviously closer together than first and second, or third and fourth, may even appear as one punctation. (Fig. 20a). Beetle large, (11 mm +). Brownish in colour. Head broad and square with angular posterior margin, with many deep punctations and hairs (aedeagus, Fig. 20b) .....*P. hospes* Erichson

21. Beetle medium to large, 8 mm +. Head broad and square (Fig. 21a) appearance black and hairy. Elytral stripe appearing at most as a brown line along elytral suture sometimes extending along the posterior margin of the elytra but never anteriorly laterally (Fig. 13c). Mesosternal process forms a definite pointed spike. (Fig. 21b). Fore coxae always dark, covered in black spines (aedeagus, Fig. 21c) .....*P. sanamus* Tottenham

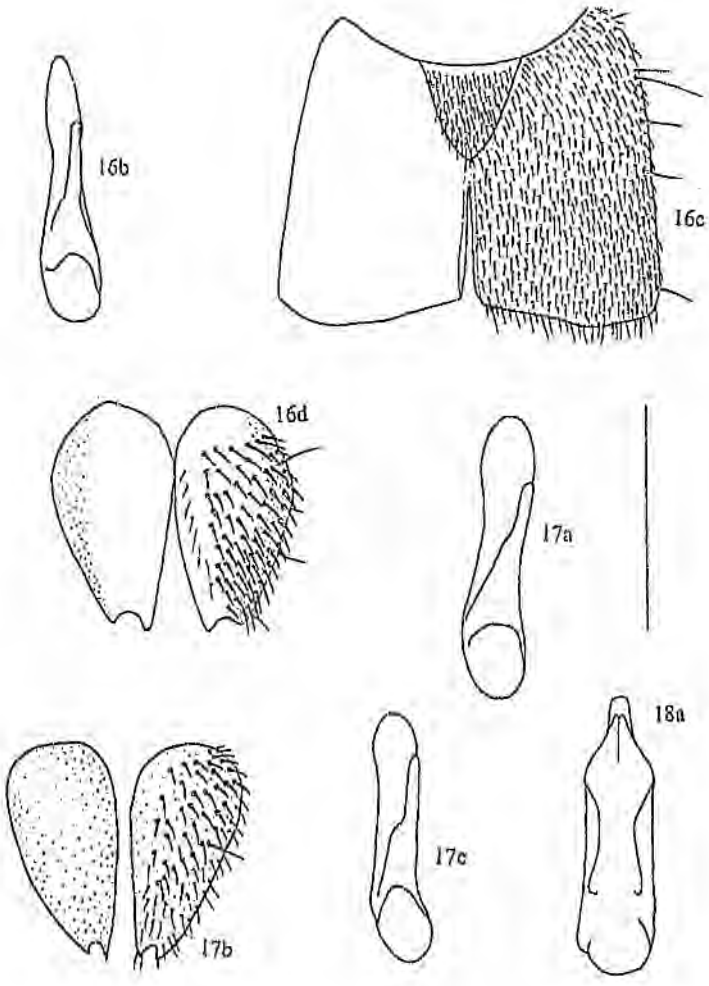
- Beetle small to medium (5 - 7 mm). Head narrow and oval, appearance slender. Elytral stripe obvious, yellow or brown often extending laterally at the posterior margin of the elytra and anteriorly laterally. Mesosternal process rounded apically (Fig. 21d). Fore coxae light on their inner surface (Fig. 21e; aedeagus, Fig. 21f) .....*P. minutus* Boheman (This may be a species complex; P. Hammond pers. comm.)



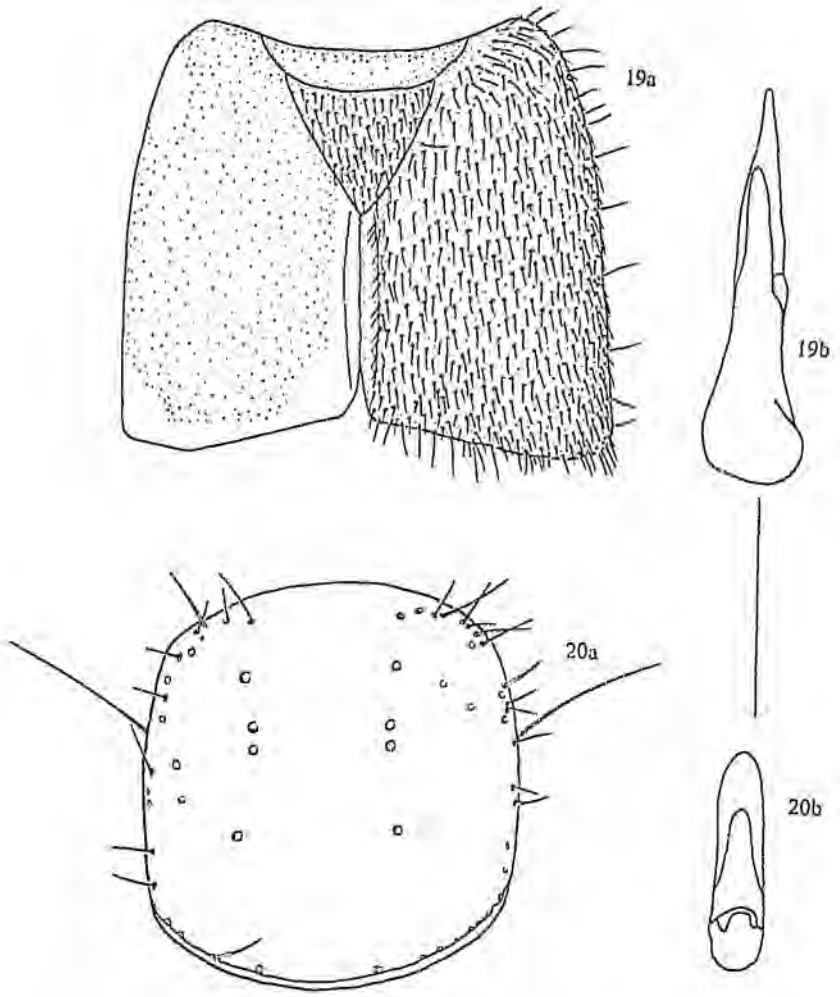
Figures 13-14. Head, elytra, fore coxae and aedeagus of *Philonthus Spp.* 13a, head of *P. bisignatus*. 13b, aedeagus of *P. incognitus*. 13c, marginal elytral line, e.g. *P. sanamus*. 13d, square-shaped head, e.g. *P. ventralis*. 14a, fore coxae of *P. ventralis*. Scale bar = 1 mm.



Figures 14-15. Heads, fore coxae, elytra and aedeag of *Philonthus Spp.* 14b, oval head shape, e.g. *P. peregrinus*. 14c, spines on fore coxae, e.g. *P. peregrinus*. 15a, aedeagus of *P. ventralis*. 15b, head of *P. morio*. 15 c, aedeagus of *P. morio*. 16a, elytra of *P. peregrinus*. Scale bar = 1 mm.



Figures 16-17. Elytra, fore coxae, pronotum mesosternum and aedeagi of *Philonthus Spp*. 16b, aedeagus of *P. peregrinus*. 16c, elytra of *P. labdanus*. 16d, fore coxae of *P. labdanus*. 17a, aedeagus of *P. labdanus*. 17b, fore coaxae of *P.incognitus*. 17c, aedeagus of *P.incognitus*. Scale bar = 1 mm.



Figures 19- 20 Elytra, pronotum and aedeagi of *Philonthus Spp.* 19a, elytra of *P. densecaudatus*. 19b, aedeagus of *P. densecaudatus*. 20a, pronotum of *P. hospes*. 20b, aedeagus of *P. hospes*. Scale bar = 1 mm.

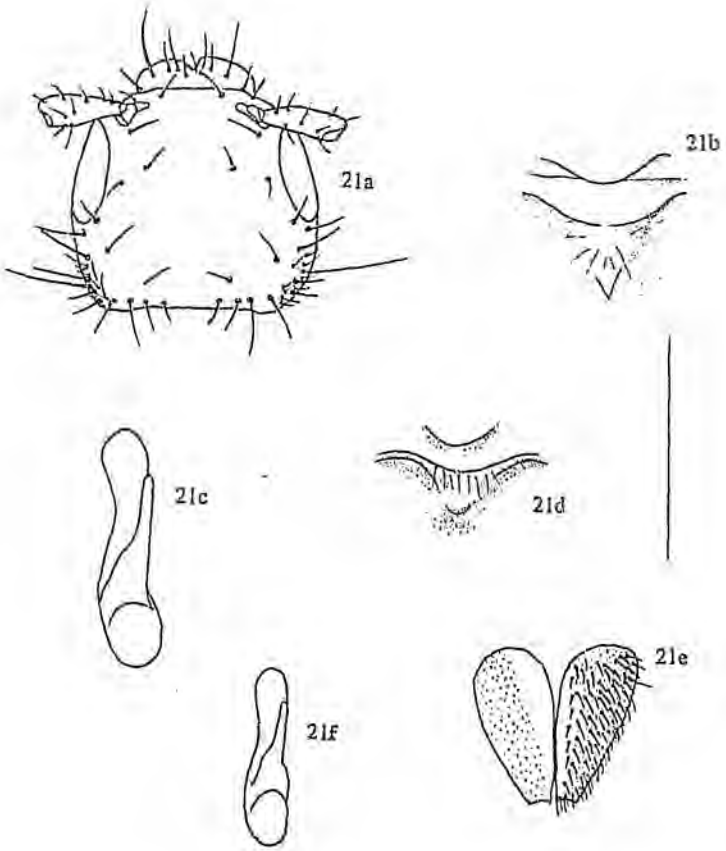


Figure 21. Head, mesosternal processes, aedeagi, and fore coxae of *Philonthus Spp.* 21a, head of *P.sanamus*. 21b, mesosternal process of *P. sanamus*. 21c. aedeagus of *P. sanamus*. 21d, mesosternal process of *P. minutus*. 21e, fore coxae of *P. minutus*. 21f, aedeagus of *P. minutus*.

2.2.3 Life history

Other than taxonomic interest and some studies of biocontrol agents of agricultural pests (e.g. Kowalski, 1976; Harris and Oliver, 1979; Andersen, 1983; Hunter *et al.*, 1989), *Philonthus* species have received minimal scientific attention. Little is known about their general biology and behaviour (Smetana, 1995), so it is worth recording what was observed in the course of this study. Illustrations of the immature stages of *P. sanamus* are given in Byrne (1993).

2.2.3.1 Oviposition

The eggs of most *Philonthus* are laid at the dung/soil interface, usually singly or occasionally in groups, (Lipkow, 1968, 1982; Eghtedar, 1970, [Europe]; Prins, 1984, [South Africa] and Hunter *et al.*, 1986, [North America]). The eggs are species specific in appearance, (Hinton, 1981), and can be usually separated from those of sympatric *Philonthus* species. With regard to the study species, *P. sanamus* eggs have ten tuberculate ridges along their length bearing aeropyles (Byrne, 1993). But *P. incognitus* and *P. labdanus* eggs each have eight ridges bearing aeropyles, and are unfortunately indistinguishable under a dissecting microscope. The exact function of the egg surface sculpture is unknown, but it may be related to respiration. Hinton (1981) suggests that elevating the aeropyles above the egg surface enables the egg to use atmospheric oxygen when covered by a layer of water, this is also given as the reason for development of the respiratory horn which is particularly long in the eggs of *Spatulonthus* species. In the laboratory, the female lays the large egg onto the substrate, usually at the dung/soil interface, but this may be due to laboratory conditions as the adult beetles cannot burrow readily. In the field they may use tunnels of other arthropods to lay eggs at any suitable position throughout the pat. The egg is held between the gonocoxites of the ninth abdominal segment and placed into a natural crevice on the surface (Fig. 22). Soil and loose dung fibers are collected in the mandibles and passed backwards through the first two pairs of legs to the hind

legs which are used to pack the material around the egg. The whole process takes about ten minutes and is accomplished with shuddering, stretching and bending motions. The purpose of this behaviour is presumably to conceal the egg, as the female does not have an ovipositor which she can insert into the substrate.

Occasionally eggs did not hatch and were consumed by fungi, but this may be because the eggs are not viable. Nematodes were often noted on the surface of eggs in the laboratory; these are generally common in dung and did not appear to affect hatching. Adult and hypopus stages of mites were sometimes found in large numbers on field caught adult beetles, adhering to the underside of the elytra; these are most probably phoretic. On rare occasions an unidentified arthropod was seen, which appears as jointed appendages sticking out of the membranes of the basal articles of the hind legs. This was suspected to be a strepsipteran. However, Hoebeke and Kovarid (1988), reported a similar looking parasite in *Quedius sp.* to be hymenopteran. A large number of entomophagous fungi have been recorded from adult *Philonthus* (Smetana, 1995).

2.2.3.2 Hatching

The mandibles of the first instar larva are visible through the egg prior to hatching. The eggs take about three days to hatch at 25°C, (Chapter 5). On hatching, the egg splits lengthways on one side, usually down one of the less pronounced longitudinal ridges, and the white larva emerges. The larva takes about six hours at 25°C to become fully chitinised.

2.2.3.3 Larvae

Philonthus have active campodeiform larvae. They are generally found at the dung/soil interface, which may be caused by laboratory conditions as the larvae cannot burrow easily, but in the field they may use the burrows of other arthropods to range through the pat (Valiela, 1969a). The larvae are carnivorous, taking any soft-cuticled prey, such as fly eggs and larvae, mites and other beetle

larvae, including their own siblings. There is some indication that the adults and larvae may also ingest dung juices, because they have been observed pushing their mouthparts into wet patches of dung when first placed onto fresh dung. Prins (1984) also noted this behaviour in *P. natalensis* adults and larvae. All species of *Philonthus* larvae observed do not consume their food whole, but pierce their prey with their mandibles and ingest the liquid contents with the aid of the labium and maxillae.

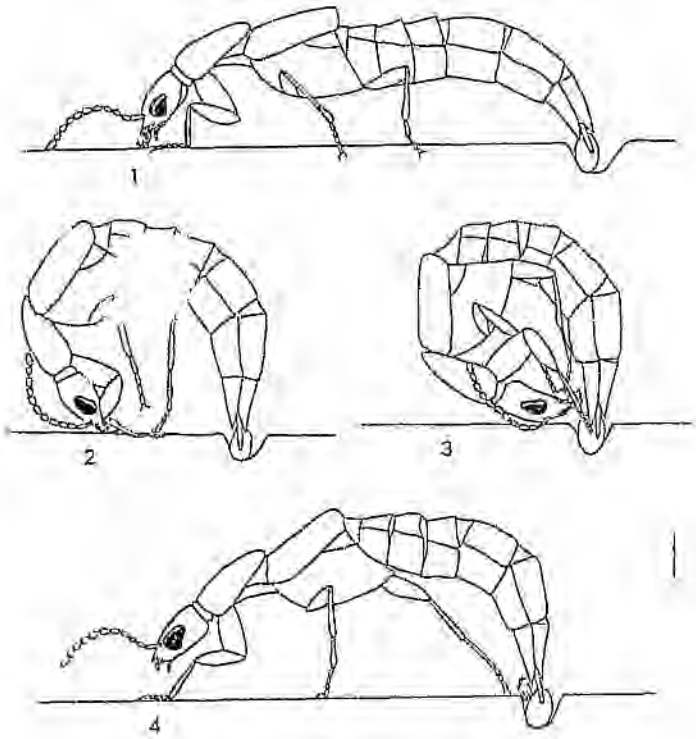


Figure 22 Oviposition behaviour of female *Spatulonthus sp.* 1) Egg held in gonocoxites; dung fibers are picked up in the mandibles. 2-3) Dung is passed back between the legs. 4) Dung fibers are packed around the egg using hind tarsi.

Adults and larvae of *Philonthus* are known to digest food extra-intestinally (Heessen and Brunsting, 1981). Crowson (1981) states that the larvae of some *Philonthus* species may possess venom glands in the head, with ducts leading to the tips of the mandibles, which are used to overpower prey by injecting them with poison.

2.2.3.4 Moulting

Moulting takes place by the skin splitting along the back of the larva and the head-capsule splitting along the dorsal ecdysial lines. The skin is shed forwards over the head and the head capsule is often left completely intact with the mandibles attached. The newly moulted larva pumps air into its body cavities and alimentary canal, with stretching and bending motions of the body causing it to swell before the new skin is fully chitinised,. The larva remains active throughout and will move away if disturbed. The head capsule is not eaten and serves as a useful indicator of moulting.

2.2.3.5 Pupation

Pupation has only been observed in the laboratory. The third instar larva constructs a pupal cell in the soil beneath the dung pat. This is achieved by lifting out soil particles with the mandibles and passing them back to the legs by sideways movements of the head. The legs then push the soil away and the animal works around the cavity, so that a circle of loose soil reveals where the larva has been digging. The final chamber is usually about 1 cm below the soil surface at a slight angle from the vertical. The chamber is usually dug beneath the dung pat in the soil that has been moistened by drainage of water from the pat. If no soil is provided pupation will take place in the dung. In a filter-paper-lined petri-dish, the third instar larva will chew up filter-paper to construct a loose fiber cell in which to pupate. The pupa is obtect and is found in a head-up position in the cell.

2.2.3.6 Emergence

The adult beetle emerges from the pupal cell beneath the dung pat and spends several hours at the dung/soil interface. The body is almost completely black, apart from the elytra which are pale and clear. The wings are unfolded and exposed. Within an hour the elytra have darkened and the wings are folded beneath them. No diurnal pattern of emergence has been noted in laboratory colonies.

2.2.3.7 Copulation

Copulation is a very aggressive and rapid procedure in the *Philonthus* species observed. The male and female appear to recognise each other without any courtship. After a brief encounter and antennation, the male mounts the female from behind, and either lies on top or alongside the female (Fig. 23). The male extrudes his genitalia, inserting the median lobe into the female, with the paramere remaining outside (Chapter 3). During the brief copulation the male constantly strokes and taps the female's dorsum with his legs and antennae.

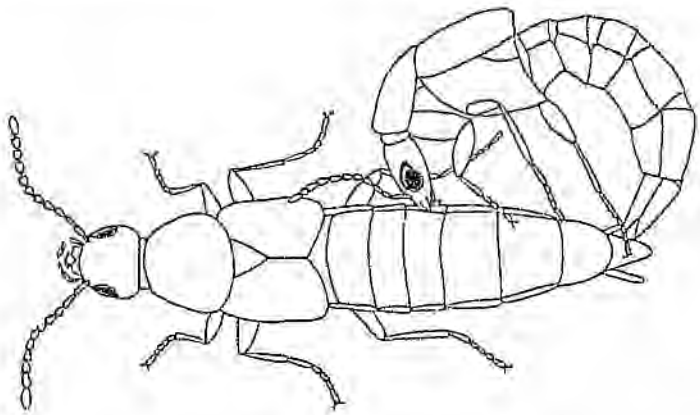


Figure 23. Copulation of *Spatulonthus sp.* In this position the male lies alongside the female. Males may also lie partially on top of the female as in figure 5, chapter 3.

2.2 Rearing

Although there are accounts of *Philonthus* beetles being reared in the laboratory (Mank, 1923; Hafez, 1939b; Harris and Oliver, 1979; Prins 1984), few of these give full details of the actual methods used. At best, the majority note that beetles were reared in petri-dishes with moist filter paper (Lipkow, 1968; Eghtedar, 1970; Boller, 1983). Methods specifically for *Philonthus* species are given by Campbell and Hermanussen (1974), and Hunter *et al.*, (1986).

For laboratory studies, cattle dung approximately two-days-old was collected from the field, and adult beetles were extracted in Berlese funnels. Captured beetles were immobilised with CO_2 and sorted and sexed under a binocular microscope.

2.3.1 Egg Collection

Eggs used for experimentation were collected from beetles maintained at 25 °C, by setting up adult beetles in pairs in 2-litre plastic containers filled with about 10 cm of damp dark soil. Approximately 200g of fresh cow dung was placed on top of the soil. The dung had been moulded into a smooth ball and dropped onto a plastic grid to create a pattern of grooves in the bottom surface of the dung, about 3 mm wide and 10 mm apart, where the beetles could hide. These grooves were painted with about 50 - 100 housefly eggs.

Beetle eggs were collected daily with a fine paint-brush, by washing the under-surface of the pat with a fine water-spray which removed soil and dung particles, exposing the white eggs against the dung. Eggs were occasionally found on the surface of the soil and for this reason fine dark soil was used as a substrate to show up the eggs more clearly. The only disadvantage of this method was that it was time consuming and eggs may have been missed in the dung which resulted in larvae being found several days later. Adult beetles were moved to new pots and fresh dung once a week.

Two basic rearing methods were used. To simply rear beetles through to adult, eggs were collected and then set up in grooves on the bottom of fresh dung patties and placed individually in pots identical to those of the adults. Housefly eggs (50-100) were added daily, and after the larva had pupated, the dung and soil were sprayed occasionally to keep them moist until emergence of the beetle.

Good survival and emergence were obtained with this rearing method. The major drawbacks of this technique were that larvae could not be closely observed for recording development without disturbance, and the method was labour intensive.

To observe larval development closely, *Philonthus* eggs were collected and set up on moist filter paper in 70 mm x 1.4 mm plastic petri-dishes, one egg per dish. Housefly eggs were added daily until the larva reached the late third instar when its abdomen becomes grossly enlarged and yellow from fat deposition. At this stage the gut is also empty, as can be seen through the body wall. The larva was then transferred to a 2-litre pot, as in the previous method, the dung having been aged from the date the eggs were collected. This allowed pupation to take place in the soil. Initially, attempts were made to make third instar larvae pupate in petri-dishes with no soil, but mortality was so high that the pot method was tried with more success.

CHAPTER THREE

VERIFICATION OF THE SPECIFIC STATUS OF *P. incognitus*, *P. labdanus* AND *P. sanamus*

3.1 Introduction

To investigate the ecology of different species sharing the same habitat one has to be able to identify each species, and be confident that their separation is valid. With experience this identification process becomes instinctive, but then it is difficult to explain to anyone else and even harder to justify, the criteria used for identification. Construction of a key is a useful exercise to help clarify the characters used to separate species, and with beetles these can usually be confirmed by the distinctive form of the male genitalia (Sharp and Muir, 1912). This holds true for most local species of the genus *Philonthus*, which exhibit great variation in the form of the median lobe of the aedeagus and in the parameres, which may be paired, fused or single, and bear tiny peg-like setae in a distinctive pattern on their inner face near the tip. However, members of the subgenus *Spatulonthus* are infuriatingly similar in external appearance and in the aedeagi which all have a spatulate median lobe, and a single asymmetric paramere with a few setae at the tip. Hammond, (1972, 1981b), has suggested that the pattern rather than the absolute number of these setae, which is variable, is a useful specific character.

Difficulty in separating adults of *Philonthus incognitus*, *P. labdanus* and *P. sanamus* created the need to make certain that the three species being studied were indeed distinct and not different morphs of a single polytypic species. Because *Spatulonthus* aedeagi appear identical and cannot be examined in females or live males, it was necessary to find other, possibly less reliable characters, such as setae and colour patterns, to separate trap catches and sort material for laboratory studies

(Chapter 2). To allay criticism that this could merely result in division of different local forms of the same species, some evidence had to be gathered to ensure that distinct species had been identified. Two methods were used, comparison of particular structures on each species, and comparison of intra- and interspecific mating behaviours of the three species, particularly willingness to mate. Mating behaviour is commonly used to assist in recognition of cryptic or sibling species, (Walter, 1993; Helmpel *et al.*, 1997).

Even if the study species had been separated correctly there remains the problem of assigning them a name from the confusion surrounding members of *Spatulonthus* in general. Tottenham (1955) suggested that these difficulties would not be resolved until long series of all the groups became available. Such series are still not available. Examination of the material in the Natural History Museum (London) in 1995, (4 *P. incognitus*; 12 *P. labdanus* and 21 *P. sanguus*) did not resolve the issue and this confusion persists, with much apparent overlap in the appearance of the three species. This may be exacerbated by local variation in the species, collected from a broad spread of localities yielding only one or two specimens each (Chapter 4; Appendix).

3.1.1 Mate Recognition

Animals that employ internal fertilisation typically have male genitalia that are very varied, particularly in closely related species (Eberhard, 1985). Many theories have sought to explain this genitalic extravagance, starting with the lock and key hypothesis of Dufour (1844, in Eberhard, 1985). The male genitalia are usually a perfect and complicated fit into the female, and this mechanical close fit should act as a barrier to non-specific matings. But, often the lock can actually be picked by many keys, and the corresponding variety in the female genitalia predicted by this hypothesis does not occur (Hammond, 1981a). Pleiotropic effects, where genes coding primarily for other characters secondarily influence the form of the genitalia,

have been suggested to explain the variety of male aedeagi. But this is probably the least convincing theory. Elaboration of the genitalia is not seen in animals that use external fertilisation, but is common in the other body parts used for intromission such as the pedipalps of male spiders (Eberhard, 1990). An alternative hypothesis supposes that the genitalic structure results from male to male competition, where the genitalia are used to dislodge or displace sperm from earlier matings with other males. While this is certainly true for damselflies (Waage, 1979), most male intromittent organs do not penetrate to where the sperm is stored or used, to be able to dislodge it (Eberhard, 1985). The most viable theory on the subject to date is that of sexual selection on the male genitalia by female choice. The male genitalia are proposed to act as an internal courtship mechanism to stimulate the female to accept and use the sperm of a particular male (Thornhill, 1983). This would lead to strong sexual selection on the male genitalia, resulting in rapid and radical divergence of form (The Fisher effect, Eberhard, 1990; Andersson, 1994), which is what is generally seen in most species of closely related insects where the females mate more than once.

Hammond (1972, 1981b) described the pattern of peg-like setae on the paramere of the male aedeagus of Staphylinidae as species-specific and suggested that they play some role as specific mate recognition signals. Jepson (1981, 1984), tested this idea by observing mating behaviour in two species of *Philonthus*. She concluded that the pegs are redundant as prezygotic mating barriers because the paramere does not enter the female during copulation, however she did not look for tactile receptors on the abdominal sclerites of the female that would correspond to the position of the paramere during copulation. Peg-like setae are found on various external parts of some staphylinids and serve as secondary sexual characteristics (Hammond, 1972). Peschke (1978a, 1978b,1979) studied the mating behaviour of *Aleochara curtula* (Staphylinidae) in detail, and found that a combination of pheromones and tactile signals, including distribution of setae, play an important role in courtship and mating.

If, contrary to the broadly accepted function of the male intromittent organ as a device primarily for transferring gametes, "internal courtship" of the female is the main role of the male genitalia (Eberhard, 1996), then the pressure to evolve divergent genital morphologies should be strongest within closely related species sharing the same habitat (Eberhard, 1990). This divergence has not occurred between the species of *Philonthus* under study, as the genitalia are almost identical, unless the patterns of peg-like setae on the parameres are radically different and play some role in copulation. Because the absolute number of pegs on any one species varies quite considerably, Hammond (1972, 1981b) assumes that the pattern of the pegs is used as a species mate recognition signal. Insect species that have nondescript genitalia, generally display elaborate courtship rituals and females only mate once (Eberhard, 1985, Walter, 1993). This removes the opportunity for post-copulatory choice and lends support to Eberhard's theory. In the light of the above and the frustrating similarity of the male aedeagi of the beetles in question, one should be able to predict that the study species will have an elaborate species specific precopulatory courtship followed by a single insemination of the female.

To ensure that *P. incognitus*, *P. labdanus* and *P. sanamus* are valid non-interbreeding species, their genital morphology was compared, and mating behaviour observed and quantified to reveal similarities and differences between the species to see if they could, or would interbreed.

3.2 Methods

3.2.1 Morphology

Adult beetles were collected from the field and separated into species according to described morphological characters (Chapter 2). This separation was validated by

A. Smetana at Biosystematics Research, Agriculture, Canada. He confirmed the identity of *P. sanamus* Tottenham and determined that of the two other species. The first, known to the CSIRO Dung Beetle Research Unit (DBRU) in Pretoria, as *Philonthus maskinius* Tottenham (Davis *et al.*, 1988), Smetana identified as *P. labdanus* Tottenham, and the second he identified as *P. incognitus* Bernhauer. He did, however, state that he was not that familiar with the African fauna, (Smetana, pers. comm.).

Laboratory-reared beetles were killed and preserved in alcohol, then dissected and examined for specific characters using a scanning electron microscope (SEM). Aedeagi were removed from eight males of each species, four were mounted intact and four had the paramere removed so that its inner face could be seen. Specimens of the eighth, ninth, and tenth tergites and sternites of both sexes were also mounted for examination. All material was mounted with graphite onto stubs, air-dried at 50°C and coated with gold palladium. These were viewed with a JEOL scanning microscope at 10-15 kV, using magnifications of x100 to x10,000. Drawings were made from electron micrographs.

3.2.2 Mating Behaviour

Sexually mature beetles were obtained from laboratory stocks and kept separately at 25°C, 12-24 hour light regime for at least 24 hours prior to use. Observations of intra- and interspecific behaviour of males and females of all species were made in 9 cm clear perspex petri dishes, with the floor of the dish covered with damp filter paper. A male and female were placed in the dish at the start of the trial. Each trial lasted 10 minutes or until copulation had taken place. Behaviour was divided into 10 activities as listed below (Jepson, 1984), which were recorded as they occurred, and duration of copulation was recorded.

Exploratory	1. Examination of the female abdominal apex by the male. 2. Examination of the male abdominal apex by the female. 3. Prolonged examination and antennation of the female by the male.
Copulatory	4. Mounting by the male. 5. Extrusion of male genitalia. 6. Intromission.
Aggressive	7. Aggression by the female. 8. Aggression by the male. 9. Avoidance by female. 10. Avoidance by male.

These categories did not necessarily all occur, or follow each other in the sequence listed above. Observations were made at 25 °C under artificial light. The following groups of interactions were observed:

Intra-specific

1.	♂ *P. incognitus*	x	♀ *P. incognitus*
2.	♂ *P. labdanus*	x	♀ *P. labdanus*
3.	♂ *P. sanamus*	x	♀ *P. sanamus*

Inter-specific:

4.	♂ *P. incognitus*	x	♀ *P. labdanus*
5.	♂ *P. incognitus*	x	♀ *P. sanamus*
6.	♂ *P. labdanus*	x	♀ *P. incognitus*
7.	♂ *P. labdanus*	x	♀ *P. sanamus*
8	♂ *P. sanamus*	x	♀ *P. incognitus*
9.	♂ *P. sanamus*	x	♀ *P. labdanus*

Twenty replicate trials for intraspecific pairings, and 10 replicate trials for interspecific pairings were carried out. The behavioural components of the courtship process were used for quantitative comparison of intra- and interspecific behaviour. The total number of times a particular behaviour occurred was recorded for each trial, and the mean occurrence of the most common behaviour in each category was compared across the species using a one-way ANOVA.

3.3 Results

3.3.1 Morphology

Live specimens of the species under study were separated by the characters given in Chapter 2. Even under SEM the complete aedeagi of all three species are indistinguishable (Fig. 1). The parameres differ slightly, but this varies amongst individuals of the same species and with the angle at which the aedeagus is viewed. The pegs on the inner face of the paramere differ in appearance within and between species. The paramere of *P. incognitus* generally has 10 pegs in two rows (Fig. 2). *P. labdanus* specimens were found with eight, nine or 10 pegs in two rows towards the lateral margins of the tip. The pegs may be reduced or present as a hair. *P. sanamus* has six pegs at the tip in two rows of three, the proximal pair being

reduced. The distribution of the pegs was not notably symmetrical in any of the species.

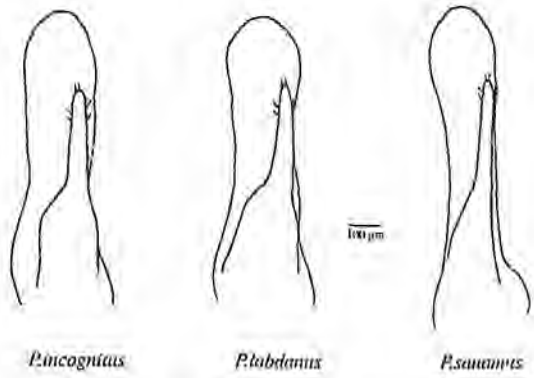


Figure 1. The spatulate aedeagi of three *Philonthus* species. Note the single asymmetric paramere

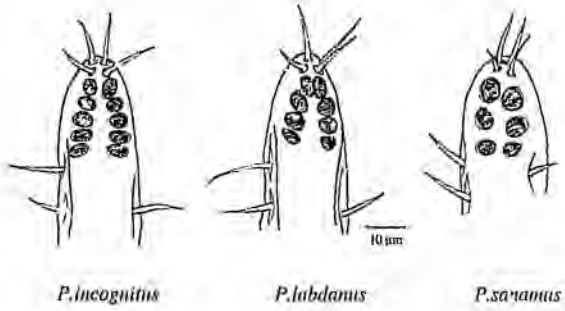


Figure 2. Peg-like setae on the inner distal face of the paramere of three *Philonthus* species

During courtship, male *Spatulonthus sp.* appear to examine the tenth tergite of the female. SEM revealed no major differences in the distribution of hairs in this region except that *P. labdanus* has seven stout hairs near the apex of the segment with two being placed proximally medially, while the other two species have six stout hairs (Fig. 3).

Ventrally, the second gonocoxites appear very similar in all species. Small peg-like setae, similar to those shown by Hammond (1972), are found on the medial surfaces. (Fig. 4).

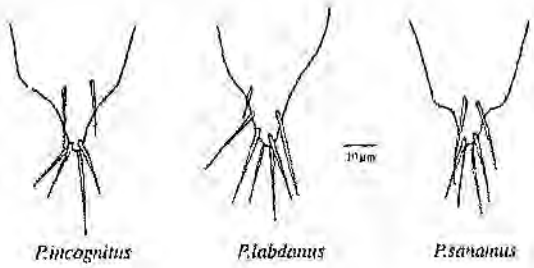


Figure 3. The apical portion of the tenth abdominal tergite of three female *Philonthus* species

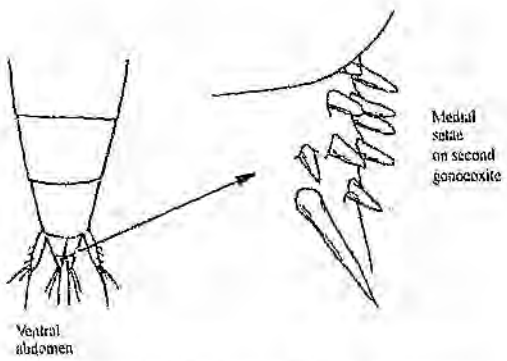


Figure 4. Sensory setae on gonocoxite of a female *Philonthus sanamus*

3.3.2 Mating Behaviour

The behavioural components of intra-specific behaviour described by Jepson (1984) proved adequate in describing and categorising beetle interactions for these trials.

Figure 5 illustrates the main behaviours identified from observation of beetle pairs. Behavioural categories used in the analysis are numbered one to 10 and a brief description of them is given below.

Antennal fencing

Copulation is most frequently initiated by the male and female meeting face to face. This happens apparently by chance, as the beetles seem unaware of each other's presence in the petri dish until they bump into each other, when antennation by both sexes occurs. The female may raise her abdomen to indicate receptiveness, but because this is also a defensive posture adopted by both sexes of many genera of staphylinids (Alcock and Forsyth, 1988), it is difficult to distinguish receptiveness from defence.

Male and female interactions

1. Examination of female abdominal apex by male. The male antennates and palpates the female abdominal apex.

2. Examination of male abdominal apex by female. This infrequently took place in intraspecific pairings (Fig. 6), but was common in interspecific pairings (Fig. 7).

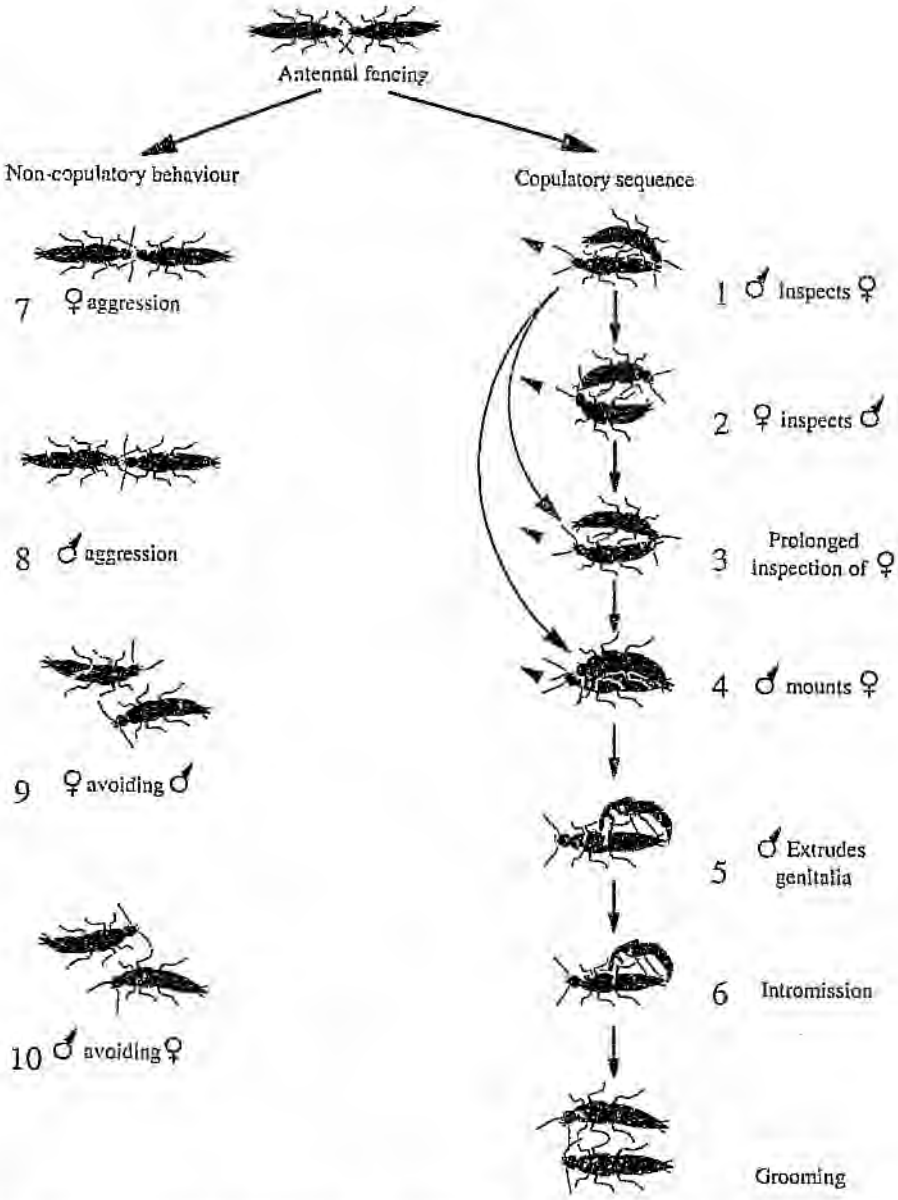


Figure 5. Diagrammatic representation of mating behaviour in *Philonthus spp.* Categories used for descriptive and comparative purposes are numbered one to 10. Details of each category are provided in the text.

3. Prolonged examination and antennation of female by male. This exploration of the female abdominal surfaces was generally a strong indication that copulation was about to take place in intraspecific pairings.

4. Mounting by male. Either on top of or alongside female.

5. Extrusion of male genitalia. The male genitalia are extruded before insertion into the female. Either sex may still terminate courtship at this stage.

6. Intromission. The median lobe of the male aedeagus is inserted into the female genital orifice, the male may continue to antennate the female. The female is generally still during this phase. Which sex terminates copulation is unclear, after retraction of the male genitalia, the pair usually separate and the female moves the gonocoxites of her ninth abdominal segments laterally and alternately towards the body mid-line. Self grooming generally follows.

7. Aggression by female. When the female actively attacks the male with mandibles open and attempts to bite.

8. Aggression by male.

9. Avoidance by female. One of the beetles will actively move away from the other or change its direction of walking to avoid contact with the other.

10. Avoidance by male.

These behaviours do not always necessarily follow one another in the sequence above. Figures 6 and 7 summarise the occurrence of the different behaviours in intra- and interspecific trials.

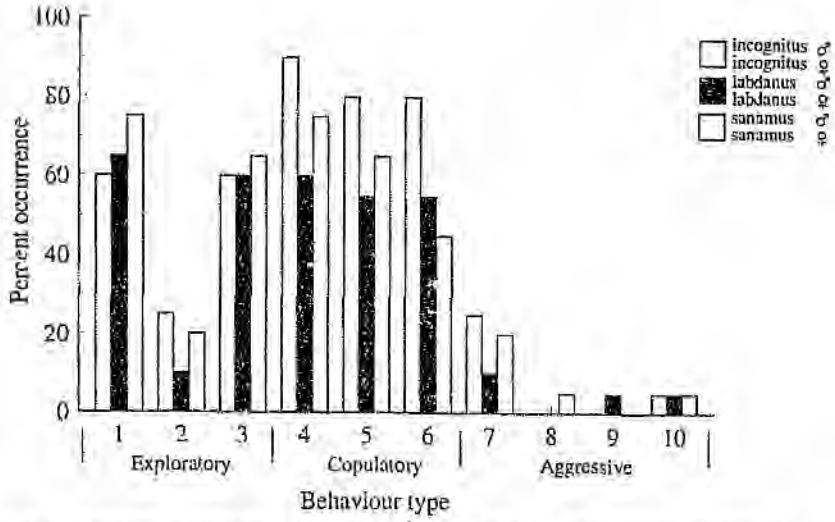


Fig. 6. Summary of intraspecific mating behaviour in three species of *Philonthus*. 1 = ♂ inspects ♀, 2 = ♀ inspects ♂; 3 = prolonged ♂ inspection of ♀; 4 = ♂ mounts ♀; 5 = ♂ extrudes genitalia; 6 = intromission; 7 = ♀ aggression; 8 = ♂ aggression; 9 = ♀ avoiding ♂; 10 = ♂ avoiding ♀.

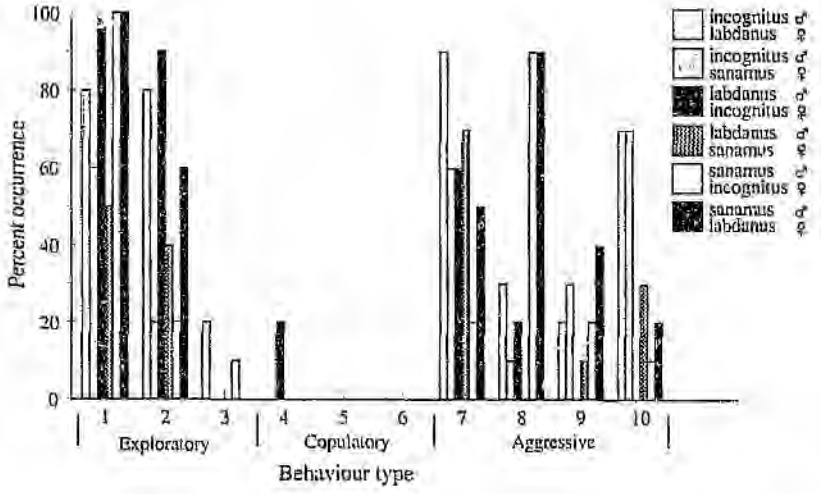


Fig. 7. Summary of interspecific mating behaviour in three species of *Philonthus*. 1 = ♂ inspects ♀; 2 = ♀ inspects ♂; 3 = prolonged ♂ inspection of ♀; 4 = ♂ mounts ♀; 5 = ♂ extrudes genitalia; 6 = intromission; 7 = ♀ aggression; 8 = ♂ aggression; 9 = ♀ avoiding ♂; 10 = ♂ avoiding ♀.

Intraspecific behaviour.

1. ♂ *incognitus* x ♀ *incognitus*

The male examined the female abdominal apex in 60% of trials, this usually led to prolonged examination and the sequence of events leading to intromission. Intromission was achieved in 80% of trials. Aggression was infrequent and only from females.

2. ♂ *labdanus* x ♀ *labdanus*

Intromission was achieved in 55% of trials following the sequence of male examination and mounting of the female. Female aggression was rare.

3. ♂ *sanamus* x ♀ *sanamus*

More males (75%) examined females than in the other species, but achieved fewer copulations (45%). Female aggression was infrequent.

All species showed significantly different copulation times ($F = 264.579$, $df = 2,94$; $P = 0.000$), with *P. sanamus* copulation being dramatically shorter than the other species (Table 1). Individuals that did not mate in these trials were noted and later paired with other beetles of the same species. In all cases they copulated with conspecific mates.

Table 1. Duration, in seconds, of copulation in three species of *Philonthus*. n = number of observations made.

	P. incognitus	*P. labdanus*	*P. sanamus*
mean duration (seconds)	11	9.6	3.8
std. dev.	2.3	1.5	0.68
range	8.5-15	6-11.5	3-6
(n)	40	27	30

Interspecific Behaviour

Figure 7 summarises the behaviour of interspecific pairs, Tables 2, 3 and 4 compare the occurrence of behavioural activities in these trials with that recorded for intraspecific pairings. The overall pattern, and main difference from the intraspecific trials, was an increase in inspection of abdominal apices, particularly by females, the complete absence of interspecific copulation and the increase in aggression.

1. ♂ *incognitus* x ♀ *labdanus* or ♀ *sanamus* (Table 2)

Initial inspection by the male was similar for all females, but prolonged examination of the female occurred significantly less often than observed in the intraspecific trials. The sequence leading to intromission did not occur with females of *labdanus* or *sanamus*, who were more aggressive in response to *incognitus* males than their conspecifics, causing the males to avoid them.

2. ♂ *labdanus* x ♀ *incognitus* or ♀ *sanamus* (Table 3)

Initial contact, and female examination of the male was greatest between *labdanus* and *incognitus*, but prolonged examination was again significantly less than for the conspecific females in trial 1. Male *labdanus* mounted female *incognitus* several times in two trials but the females shook them off violently and attacked them. Female *incognitus* and *sanamus* were most aggressive to male *labdanus*, while avoidance behaviour in the male *labdanus*, female *sanamus* pairings was significantly high.

Table 2. Summary of one-way ANOVA results of mean occurrence of behavioural components during interspecific mating trials of three species of *Philonthus*. *P. incognitus* males x intra- and interspecific females. Test statistics followed by the same letter are not significantly different at the 0.05 level, Tukey HSD.

Behaviour	P value	♂ *P. incognitus* x ♀ *P. incognitus*	♂ *P. incognitus* x ♀ *P. labdanus*	♂ *P. incognitus* x ♀ *P. sanamus*
♂ inspects ♀	0.724	0.9 a	1.2 a	0.9 a
♀ inspects ♂	0.000	0.3 b	1.6 c	0.2 b
♂ inspection of ♀	0.002	0.7 d	0.2 e	0.0 e
♂ mounts ♀	0.000	1.5 f	0.0 g	0.0 g
♂ extrudes genitalia	0.000	0.8 h	0.0 i	0.0 i
intromission	0.000	0.8 j	0.0 k	0.0 k
♀ aggression	0.018	0.5 l	3.1 m	1.5 l m
♂ aggression	0.046	0.0 n	0.5 o	0.1 no
♀ avoiding ♂	0.075	0.0 p	0.3 p	0.4 p
♂ avoiding ♀	0.000	0.0 q	0.9 q	2.3 r

3. ♂ *sanamus* x ♀ *incognitus* or ♀ *labdanus* (Table 4)

Again when compared with the intraspecific trials, initial contact was greater, and prolonged examination less, for interspecific pairs. No mounting or copulatory behaviour took place in these pairings. Female aggression was low, but male aggression towards non-conspecific females was significantly high.

Table 3. Summary of one-way ANOVA results of mean occurrence of behavioural components during interspecific mating trials of three species of *Philonthus*. *P. labdanus* males x intra- and interspecific females. Test statistics followed by the same letter are not significantly different at the 0.05 level, Tukey HSD.

Behaviour	P value	♂ *P. labdanus* x ♀ *P. labdanus*	♂ *P. labdanus* x ♀ *P. incognitus*	♂ *P. labdanus* x ♀ *P. sanamus*
♂ inspects ♀	0.000	0.6 a	3.0 b	0.7 a
♀ inspects ♂	0.000	0.1 c	2.5 d	0.4 c
♂ inspection of ♀	0.000	0.6 e	0.0 f	0.0 f
♂ mounts ♀	0.112	0.6 g	0.7 g	0.0 g
♂ extrudes genitalia	0.000	0.5 h	0.0 i	0.0 i
intromission	0.000	0.5 j	0.0 k	0.0 k
♀ aggression	0.113	0.3 l	1.4 l	4.8 l
♂ aggression	0.145	0.0 m	0.2 m	0.0 m
♀ avoiding ♂	0.039	0.0 n	0.0 n	0.1 o
♂ avoiding ♀	0.000	0.2 p	0.0 p	0.5 q

Table 4. Summary of one-way ANOVA results of mean occurrence of behavioural components during interspecific mating trials of three species of *Philonthus*. *P. sanamus* males x intra- and interspecific females. Test statistics followed by the same letter are not significantly different at the 0.05 level, Tukey HSD.

Behaviour	P value	♂ *P. sanamus* x ♀ *P. sanamus*	♂ *P. sanamus* x ♀ *P. incognitus*	♂ *P. sanamus* x ♀ *P. labdanus*
♂ inspects ♀	0.002	1.3 a	3.9 ab	4.3 b
♀ inspects ♂	0.082	0.2 c	0.2 c	0.7 c
♂ inspection of ♀	0.000	0.9 d	0.1 e	0.0 e
♂ mounts ♀	0.000	1.0 f	0.0 g	0.0 g
♂ extrudes genitalia	0.000	0.7 h	0.0 i	0.0 i
intromission	0.000	0.45 j	0.0 k	0.0 k
♀ aggression	0.799	0.6 l	0.3 l	0.5 l
♂ aggression	0.000	0.0 m	3.5 n	1.7 o
♀ avoiding ♂	0.117	0.0 p	0.5 p	0.4 p
♂ avoiding ♀	0.455	0.0 q	0.1 q	0.2 q

3.4. Discussion

3.4.1 Morphology

From the above results it is clear that the external characters used to separate *P. incognitus*, *P. labdanus* and *P. sanamus* are reliable specific differences in addition these characters have been found to breed true in laboratory populations. *P. sanamus* is the most different of the three species, *P. incognitus* and *P. labdanus* are similar enough to originally be identified by workers at the DBRU as one species.

Female morphology is disappointingly similar in that no obvious specific characters were found on the abdominal sclerites examined. Eberhard (1985) interprets

conformity in female reproductive structures as evidence of weak sexual selection on these structures found in the partner with the greatest parental investment, nevertheless he illustrates specific differences in the hemisterna of *Macrodactylus spp.* (Melolonthinae) (Eberhard, 1993). If females can discern between "good" and "bad" copulators of the same species as Eberhard suggests, then there must be a mechanism involving a physical structure of some sort to do this. Further, one would expect such a structure to have evolved to fulfil its role efficiently and therefore be species specific, taking the argument full circle. However it is probably not worthwhile looking inside these female *Philonthus* for an equivalent structure as it is virtually impossible to separate the males on genitalic characters, making it unlikely that female structures are any more different.

After antennation, male and female *Spatulonthus* of these species begin most encounters h mining the apex of the abdomen of their partner. The setae in this area are sometimes useful as specific characters, but for many species are variable in the number and location of the setae (Smetana, 1995). No obvious species specific signalling structures were found on these female's abdomens, but receptor-like structures were discovered between the second gonocoxites. These are most likely involved in oviposition rather than copulation. During oviposition the female *Philonthus sp.* holds a single egg between the gonocoxites while she packs dung fibres around the egg to conceal it (Chapt. 2). Hammond (1972) proposed that peg-like setae on the body surface of some Staphylinidae have a potential function as mate recognition signalling devices. Robertson and Paterson (1982) found what look like mechanoreceptors on the mesostigmal plate of female *Enallagma* damselflies, where the male clasps the female with his caudal appendages during mating. Females were able to discriminate between undamaged males and those that had a portion of their superior anal appendage removed. The behavioural data presented here show that such a recognition system is unlikely to operate within *Spatulonthus sp.* as mate rejection occurs long before any potential contact between the setae found on the female gonocoxites and the male paramere.

The similarity of the *Spatulonthus* aedeagi runs contrary to what is expected from closely related species living in close contact (Hammond, 19[illegible]a; Eberhard, 1990). Both authors note elaboration of the specific mate recognition system and/or male genitalia under such circumstances. Hammond (1981a) sees aedeagi and related structures as reproductive barriers of the mate rejection type, while Eberhard interprets them as internal courtship structures for enhancing male mating success. Both use the divergent structure of the male genitalia to support their hypotheses. In the light of this study, Hammond's argument seems the more improbable because interspecific intromission is not achieved. This is supported by Jepson (1984) who found that neither *P. cephalotes* nor *P. sordidus* males inserted the paramere into non-specific females during copulation. There is another structure on the male genitalia which could be an internal signalling device which was not investigated here. On the median lobe (reverse face to paramere face) of the aedeagi of all three species, there is a soft eversible sac, this not often seen and rarely illustrated (Levasseur, 1971,1980; Smetana, 1995). Eberhard (1993) has identified the eversion of a similar structure as critical to transfer of sperm in *Macrodactylus spp.* and described it as a "foot in the door" mechanism to force open the female genital chamber. But, comparing this sac in three species of the genus *Macrodactylus*, Eberhard (1993) noted no specific differences, and Smetana (1995) states that the sac is usually simple in *Philonthus*, therefore it is reasonable to suppose that this is also the case in *Spatulonthus*.

3.4.2 Mating behaviour

Eberhard (1985) makes other generalisations about reproductive morphology and behaviour that have some bearing on the results of these trials. Firstly, Eberhard predicts that more elaborate penis morphology is expected in species in which the female is more likely to mate with more than one male. In this study, multiple female matings were observed in all three *Philonthus* species, with one female

accepting as many as five consecutive males, separated only by the seconds it took to remove and replace the mated male. Multiple matings may not be uncommon in the genus because *P. fuscipennis* have been recorded copulating 30 - 35 times a day (Eghtedar, 1968). Multiple intromissions with the same males were observed in the study species (up to six in a 30 minute period) but none longer than 15 seconds. This seems to be exceptionally quick, as duration of copulation for *P. fuscipennis* is 28 - 48 seconds (Eghted r, 1968) and for *P. cephalotes* and *P. sordidus* is 86 seconds, and up to 480 seconds respectively (Jepson, 1984). Although not tested, little female choice, as defined by : ale discrimination rather than male competition, appeared to be exercised, unless it is a "cryptic choice", (Eberhard, 1996), where the female allows copulation, but blocks or otherwise selects against sperm from a particular male (Wirtz, 1997; Price, 1997). The female genitalia of *Aleochara sp.* (Staphylinidae), have complex genital tracts and the spermatheca can be used as a specific character (e.g. Klimaszewski and Jansen, 1994), so this could possibly be true in *Philonthus*, but unlikely, as previously discussed. Other differences in the two mating systems are also important to consider; copulation is prolonged in *Aleochara* species, the males produce spermatophores, and females actively discriminate against males who mate more than twice in 24 hours (Peschke, 1987), none of which was seen in these *Spatulonthus sp.*

If the aedeagi of these *Philonthus* species are redundant or non-functional as reproductive barriers to interspecific matings, then the species in question must be able to discriminate between potential mates before intromission, by either tactile or pheromonal signals or a combination. From the beetle's behaviour it appears that these signals are found on the dorsal abdomen, particularly near the apex. Peschke (1979) removed dorsal setae from female *Aleochara curtula*, confusing prospective mates as to which end was which. Short range pheromones have been found in other dung-dwelling Coleoptera (Houston, 1986), which is surprising as dung volatiles might be expected to swamp any other chemical signals. On the other hand, dung odour is almost certainly used as a long range attractant to bring

conspecifics together. Other features of the dung environment such as its patchy, ephemeral nature have been described as factors favourable for the development of alternative reproductive behaviour patterns (Ridsdill-Smith, 1990). *Aleochara curtula* provides a good example again. Immature or starving males mimic female pheromones to remain on feeding sites by avoiding male aggression (Peschke, 1987), and cockroaches are known to use the same tactic (Bailey and Ridsdill-Smith, 1990).

The study species all produce a characteristic odour when stressed, which will kill them if not adequately ventilated. Aleocharinae raise their tails when disturbed and during courtship, while *Philonthus* females also use the tail-up behaviour as a threat, or it appears, as an invitation to mate. *Philonthus politus* produce defence chemicals from the pygidial gland (Bellas *et al.*, 1974) and smaller quantities of two of these compounds have been identified from the tergal gland of Aleocharinae, although the two glands are not homologous (Peschke and Metzler, 1982). These compounds are not sex specific in *A. curtula*, but when released in low concentrations by females have a synergistic effect with the female sex pheromone found all over the body in the epicuticular lipids, initiating copulatory behaviour by males. At high concentrations the same chemicals cause an alarm reaction (Peschke, 1983). Epicuticular signals are described as short range, and tergal gland secretions as long range (Peschke, 1983). Alcock and Forsyth (1988) report that *Leistotrophus versicolor* (Staphylinidae) are apparently unaware of each other's presence from 5 cm apart, so for many of the Staphylinidae, mate recognition may rely on short range or contact cues. Chemical signalling in this family of insects has been neglected despite the variety of interactions it offers, ranging from intra- and interspecific contact to myrmecophyly (Hölldobler, 1971). Two dorsal glands in *Philonthus* are candidates for intraspecific mate recognition. There is an osmeterium on the first abdominal tergite and a pygidial gland between the eighth and ninth segment (Smetana, 1995), and both areas are examined by potential mates before reacting. Dettner (1983), has characterised 27 compounds from 14 species of *Philonthus*, and

although they are considered to be defensive, given the tail-up behaviour of receptive females, it is not too difficult to imagine that some of these chemicals could have become species specific in concentration or combination. Post-copulatory courtship, such as mate guarding was not noted in the study species, but was not investigated as such. It may prove to be of interest because a variety of mate guarding tactics have been reported in other Staphylinidae, including males attacking female mates after copulation to chase them away from feeding sites and therefore other potential mates (Alcock and Forsyth, 1988).

3.4.2 Conclusion

P. incognitus, *P. labelanus* and *P. sanamus* are not sibling species, but are closely related. Sibling species complexes are to be expected in any members of a genus that exploit habitats marginally different from each other, as ecological or behavioural specialisations are more important than morphological divergences (Paterson, 1985). The rest of this study is devoted to discovery of how different the niches of the three *Philonthus* species are, and what different specialisations to these niches, if any, they exhibit.

CHAPTER FOUR

SPATIAL AND TEMPORAL DISTRIBUTION OF *P. incognitus, P. labdanus* AND *P. sanamus*

4.1 Introduction

Spatial habitat segregation has been demonstrated in many insects, from large scale distributions (Davis, 1987, 1993a; Hanski and Cambefort 1991a), down to microhabitat (Schultz and Hadley, 1987). Similar temporal partitioning has been shown in seasonal occurrence (Davis 1987) and diel activity (Tribe, 1976; Desender *et al.*, 1984; Caveney *et al.*, 1995; Cerda *et al.*, 1997; Fallaci *et al.*, 1997). The generally accepted explanations for these patterns is one of resource partitioning to avoid competition (Schoener, 1974). There are limited experimental data on competition in dung beetle communities (Giller and Doube, 1989; Hanski and Cambefort, 1991c), and what there are suggests that aggregation of potential competitors rather than separation is the norm (Giller and Doube, 1994). Differing physiologies are rarely proposed as a reason for insects occupying different habitats, and are generally given as a proximate rather than ultimate cause. Schultz and Hadley (1987) are a notable exception to this. They ascribe the microhabitat distribution of two tiger beetle species to differences in thermal tolerance; Chown *et al.*, (1995) use thermal biology and desiccation resistance to explain the macrohabitat and continental distribution of a flightless dung beetle.

4.1.1 Geographical Range

The African, or at least the southern African distribution of dung fauna in the Scarabaeidae has been fairly well worked in the last 30 years (Ferreira, 1967, 1969; Paschalidis, 1974; Tribe, 1976; Stickler, 1979; Davis, 1987, 1990, 1993a,b; Scholtz and Howden, 1987; Chown *et al.*, 1995), but very little has been done on the other three most important families of Coleoptera inhabiting dung; namely the Staphylinidae, Histeridae and Hydrophilidae. This is probably a reflection of the difficulty of working on these groups where the fauna is poorly known and most of the beetles are small, insignificant looking creatures that spend almost their whole life inside dung. However, what is known is that some of the dung fauna shows marked changes in taxonomic structure of species assemblages from temperate to tropical latitudes, with a general increase in complexity towards the warmer regions (Davis, 1990). Staphylinidae species numbers appear to change little along latitudinal gradients. Davis (1990), gives figures of 134 and 100 species, for Finland and South Africa respectively, but this may be an underestimate of species richness. Tottenham (1949a, 1949b, 1953, 1955, 1957, 1962) refers to 149 species of African *Philonthus* alone and the staphylinid fauna is generally considered to be not well known (Tottenham 1955; Smetana, 1995; P. Hammond, pers. comm.). Opposing the possible influence of increased complexity at lower latitudes are the ecological effects of extensive seasonal dung burial by scarabs in the Afrotropical region, which may cause major disturbance of pat-dwelling species (Roth, 1983).

Comparison of coprophilous dung faunas from the southern Cape, Transvaal and Kenya revealed three broad groups of species distributions; East African endemic, East African and southern African range and pan-African distribution (Davis, 1990; Davis and Dewhurst, 1993). Few of the pan-African group were intertropical (East to West distribution), and all were highland species (Davis and Dewhurst, 1993). Significant separation of fauna along altitudinal and rainfall gradients was shown, with centres of distribution of species groups separated by 75-410 m above sea level

(Davis and Dewhurst, 1993). Martin-Piera and Lobo (1993) attributed scarabaeid distribution in Europe to altitude effects, but also concluded that the mountains had not been a barrier to dispersal of beetles in the Iberian Central System (Martin-Piera and Lobo, 1992). Dung fauna has been allowed to spread north to south along the African continent by oscillating weather cycles that created pathways along open grassland areas through central Africa (Davis, 1990).

4.1.2 Macrohabitat

Specialisation is common in dung inhabiting beetles, particularly amongst African dung beetles (Hanski and Cambefort, 1991a). Specialist dung beetles are thought to have evolved in the Mesozoic, with the modern dung beetle taxa diversifying as mammal dung increased in size and type during the Tertiary (Davis, 1990). In the Staphylinidae, association with dung occurs at lower taxonomic levels and is taken as evidence of a more recent adaptation to a coprophilous habit in this family (Davis, 1990), although this opinion is not universally accepted (P. Hammond, pers. comm.).

The evolution and spread of large mammals and open grassland in Africa has led to a dung fauna mainly associated with unshaded macrohabitats. Habitat selection by dung beetles is strongly influenced by vegetation (Howden and Nealis, 1975; Hanski and Koskela, 1977; Peck and Forsyth, 1982; Doube 1983; Davis *et al.*, 1988). But this effect is often difficult to separate from the influence of soil type which generally dictates the vegetation type. Soil type is defined primarily by grain size and mineral composition, which influence the water retention and hardness of the soil. Moisture content of soil affects nesting behaviour in dung-burying Copri (Rougon and Rougon, 1983; Davis, 1989), and the survival of immature stages (Osberg *et al.*, 1993, [Scarabaeinae]). Soil type has been shown to influence the distribution of dung beetles (Doube, 1983; Davis *et al.*, 1988; Osberg and Hanrahan, 1993; Davis, 1996a), but the exact cues used by the beetle to select its habitat are

unclear. Light intensity is the most obvious candidate (Doube, 1983), but this is not the sole cue for most species, some bush species can be drawn out into the open under shade structures, while other species remain in the vegetated areas, possibly reacting to other associated parameters such as air temperature, herbage layer and leaf litter (Byrne, unpublished data). Temperature may be the single most important factor influencing pat microclimate, but is inevitably inseparable from the effects of vegetation. Dung burial is greatest on unshaded sand and least on shaded clay (Davis *et al.*, 1988). Dung-dwelling *Philonthus sanamus* have been shown to have a significant association with unshaded sites, and no association with a particular soil type (Davis *et al.*, 1988), *P. labulatus* has a similar distribution (Davis, 1996a) and *P. incognitus* was not recorded in either of these studies but would be expected to be similar in its requirements.

4.1.3 Microhabitat

Spatial separation in dung as a microhabitat can occur at many levels. Dung as a resource is patchy in its distribution and dung types can be divided into carnivore, omnivore and herbivore; the latter can be further divided into non-ruminant (coarse) and ruminant (fine). The dung fauna shows varying degrees of specialisation, with coprophages strongly associated with dung type at higher taxonomic levels (Halffter and Edmonds, 1982; Peck and Forsyth, 1982; Doube, 1987) and predators such as Staphylinidae and Histeridae showing only broad specialisation at the species level (Davis, 1994). Many dung-dwelling species are microhabitat and dietary generalists (Hanski and Koskela 1979; Hanski and Hammond, 1986). The species in the present study were not found to be significantly associated with any particular detritus type, from carrion through to rotten fruit (Davis, unpublished data), and other conspecific *Philanthus* were concluded to be "dung generalists with a slight bias to cattle dung" (Davis, 1994). Therefore it is assumed that the three species of *Spatulonthus* under study typically occur in cattle dung.

The Scarabaeidae partition the pat as they sequester dung for feeding and breeding. The Staphylinidae do not remove dung, and have only been observed constructing burrows as larvae, in which to pupate. Therefore they are largely restricted to tunnels made by other beetles, including Histeridae and Hydrophilidae, to range through the dung (Valiela, 1974), and so they will be affected by the behaviour of these other beetles. Marked temperature gradients develop in unshaded dung pats during summer (March and Bay, 1983; Byrne, unpublished data). Lumaret and Iborra (1996), found seasonal differences in the vertical distribution of *Aphodius spp.* in accumulations of sheep dung, which they concluded was evidence of behavioural thermoregulation. In tropical habitats the dung surface temperature approaches 60°C, while the base remains close to 35°C (Byrne, unpublished data). Horn fly larvae have been shown to respond to this gradient by migrating up and down within the pat during the day (March and Bay, 1983). These factors provide for potential vertical segregation of pats by dwellers as they track prey items or preferred temperatures up and down through the pat.

4.1.4 Temporal separation

4.1.4.1 Seasonal distribution

Seasonal separation of insects sharing the same habitat can often be demonstrated and is usually attributed to resource partitioning (Koskela and Hanski, 1977; Holter, 1982; Yasuda, 1984), but considerable overlap may also occur in the same community (Hanski, 1980a, Giller and Doube, 1994). There may also be latitudinal differences in this regard, because the activity of most species is fairly well spaced out along the seasonal axis in temperate dung beetle communities, while subtropical assemblages are highly seasonal. Specialist dung fauna, mainly coprophages, show greatest activity during warm wet periods (Hanski and Koskela, 1977; Ridsdill-Smith and Matthiessen, 1988; Davis *et al.*, 1988; Davis, 1995, 1996b). This activity may cease or be reduced during the winter. For carnivorous dung fauna, macrohabitat is found to be more important than season in separating species from

each other in northern temperate regions such as Finland (Hanski and Koskela, 1979). Davis *et al.* (1988) found no significant association with season or habitat for *P. sanamus* in subtropical Zululand. Three other species of Staphylininae caught in higher numbers did show an association with the rainy season. *P. laidlawi* was not caught in sufficient numbers for analysis and *P. incognitus* was not recorded in that study.

4.1.4.2 Succession

Succession in dung fauna occurs in a predictable pattern. Colonisation by coprophagous taxa is bimodal, with most dung-breeding Diptera arriving in minutes from deposition (Mohr, 1943). Coprophagous beetles arrive early (minutes to days) followed by saprophages, such as termites, which will stay up to several weeks in the dung (Hanski and Koskela, 1977; Yasuda, 1987). Predatory taxa show a unimodal colonisation pattern which persists for longer than that of coprophagous species (Koskela and Hanski, 1977; Byrne, 1988). This may be related to the build-up of prey as the dung ages. Predators such as *Philonthus* species have been shown to arrive early in the succession (day one) and remain for up to a week (Wingo *et al.*, 1974). Dependence on dung of a particular age, for food and shelter of a particular quality, may be the driving force behind co-occurrence of potential competitors, because the dung is patchily distributed and changes rapidly under the influence of the weather and other colonists. The succession may be shifted backwards and extended as the season cools. This is related to the physiological age of the dung which is strongly linked to temperature, but animals with the same requirements will still be expected to co-occur if the resources are limited.

4.1.4.3 Diel flight

Dung fauna have clear patterns of diel flight activity (e.g. Bartholomew and Heinrich, 1978; Koskela, 1979), mainly influenced by light levels or temperature, or both (Tribe, 1976; Doube *et al.*, 1988). Caveney *et al.*, (1995) have shown distinct flight patterns for beetles within the genus *Onitis*, which they suggest is a form of

resource partitioning if beetles colonise dung of a very specific age. Although many animals do defecate at particular times, such as on standing after resting, most large herbivores produce droppings throughout the day. Cattle for example, defecate on average 12 times per 24 hours (Byrne, unpublished data). This dung is also concentrated around resting areas. Sheep for instance drop 22% of their dung in 3% of their grazing area (Lamaret and Iborra, 1996). This makes such strict partitioning by dung age somewhat unlikely. Most *Philonthus* are diurnal (Smetana, 1995), as are *P. sanamus* and *P. maskinlus*, (Davis, unpublished data), and *P. incognitus* is also expected fly during the day.

4.1.4 Coexistence

Spatial and temporal co-occurrence of competitors has been shown in South African dung scarab communities (Giller and Doube, 1994), which is surprising given the ways discussed in which beetles could partition the habitat. Coexistence is the primary pre-requisite for competition to occur in the presence of resource limitation. Competition may be intense between species when it occurs, but if it is infrequent then regional coexistence is possible. There is theoretical evidence which suggests that both patchy distribution of resources and aggregated distribution of species can affect the frequency of competition and species diversity in insect communities (Shorrocks *et al.*, 1984; Ives, 1991; Sevenster, 1996). Aggregation amongst patchy resources will promote coexistence when intraspecific aggregation is greater than interspecific aggregation, with species tending to use different resource patches (Ives, 1991). Under such conditions, individuals will compete more with conspecifics than with heterospecifics (Giller and Doube, 1994). Therefore species' associations and abundance covariations within a community can be used as indirect evidence for interspecific competition (Arthur, 1987). Although such patterns cannot be attributed exclusively to competition, the causal mechanism is most likely to be interspecific competition if it is found between ecologically similar species within a trophic level (Schluter, 1984).

4.1.6 Summary

From the above review the study species would be expected to be generalist predators with a broad North to South, African distribution. They would be expected to be macrohabitat generalists associated with unshaded sites, but not with any particular soil type. Spatial microhabitat selection within sites and pats could occur along a temperature gradient. Broad seasonal distribution is expected, and early arrival in the dung succession. The three *Spatulonthus* are clearly very similar species and are expected to have the same physiological needs, therefore it is worth looking for mechanisms of resource partitioning or variance/covariance patterns in their distribution.

4.1.7 Aims

Having established *Philonthus incognitus*, *P. labdanus* and *P. sanamus* as valid species, field work was conducted to discover if they coexisted in time and space and by how much across their ranges. Spatial distribution was examined from continental distribution down to microhabitat selection of position in the pat. Temporal distribution was examined as seasonal occurrence, and position in the dung faunal succession.

4.2 Methods

4.2.1 Continental distribution

The large scale distribution of *P. sanamus*, *P. labdanus* and *P. incognitus* was investigated by collating locality data from collections of beetles at the South African Museum, Cape Town, The Transvaal Museum, Pretoria, The Natural History Museum, London and my own personal collection.

Material from The Natural History Museum (BMNH), yielded localities for 252 specimens. *P. sanamus* is easily recognisable and all 138 specimens examined were considered to be that species. The *P. incognitus* series (28 specimens) is fairly variable but unique enough to justify recording the locality data (eight localities). Difficulty was experienced in resolving any differences between *P. maskinius* and *P. labdanus*. The BMNH collection has 10 *P. labdanus* specimens from three localities. Using the key (Chapter 2) and the specific characters examined in Chapter 3, beetles under this name are indistinguishable from those under the name *P. maskinius* (76 spp., 25 localities).

The collection of named and unnamed *Philonthus* from the South African Museum, Cape Town yielded about 20 specimens each of *P. sanamus* and *P. maskinius* all of which were collected and identified by Adrian Davis. Approximately 5000 specimens of undetermined Staphylininae were examined from the extensive collection at the Transvaal Museum, Pretoria. This produced a further 30 - 40 specimens of all three species.

After examining the DBRU reference collection, I originally named my specimens *P. maskinius*. Adrian Davis, a dung beetle specialist, curated the DBRU beetle collection. He did this with assistance of Peter Hammond, a staphylinid specialist at the BMNH. Between them they identified all the DBRU southern African material as *P. maskinius*. Later, Ales Smetana a *Philonthus* specialist in Canada, determined my *P. maskinius* specimens as *P. labdanus*, but did comment that he was unfamiliar with the African fauna. As the person who has spent the most time looking at the species in question, I cannot distinguish between the two "species", and I strongly suspect that they are one and the same.

The *P. labdanus* type and six paratypes are labelled "Angola, 76·28", this and the other two localities, Muguga and Thika Rd (both in Kenya), are also shared by *P.*

maskinius. Therefore, it was decided to use the distribution data for "*P. maskinius*" in the distribution map of *P. labdanus*.

Co-ordinates were collected from locality labels, or co-ordinates for place names were generated from the Times Gazetteer of the World. Selection of specimens to generate locality data was done with extreme caution. Staphylinids in European or European-influenced collections are "carded"; stuck ventral side down onto small pieces of card which are then pinned, thus obscuring ventral characters. Therefore, if there was any doubt as to the identity of the specimen it was not included in the data set. This conservative approach to the distributions recorded was based on the premise that presence at a site yields an influential data point, while absence reveals little or nothing. Distribution maps for the three species were drawn using the "Matlab" computer programme.

4.2.2 Macrohabitat associations

Altitude

Abundance of the study species at three widely separated sites with differing elevations and temperature regimes was investigated. For one year, from March 1990 to February 1991, monthly samples were taken from Innisfree Farm, Cluny Farm and Boekenhoutskloof Farm, by collecting nine dung pats per site, of approximately two litres each, from an unshaded spot, on grass, close to a cattle kraal. Pats were selected to contain maximum numbers of *Philonthus* species. It has been previously shown (Byrne 1988), that pats 2 – 3 days old in the summer, and 5 – 6 days old in the winter will harbour the most *Philonthus* individuals. Pats were selected by estimating their physiological age from the appearance of the crust, and evidence of colonisation.

Selected pats were scooped from the substrate with the top layer of soil into individual 10 -litre bins which were sealed and returned to the laboratory, where

beetles were extracted from the pats by exposure in Berlese funnels for three days. Samples were sorted and the abundance of each species at each site was recorded for each month. Numbers of each species captured at each site were compared using ANOVA. Seasonal abundance of the three species was derived from the monthly macrohabitat data and collection data from each site were used to analyse patterns of intra- and interspecific aggregation of the three species.

4.2.3 Microhabitat selection

Dung strata

To investigate vertical habitat selection within dung pats, fresh dung was collected from the experimental pasture, homogenised and frozen. Once thawed, 30 fresh, 2L pats were made and placed in the field at Cluny Farm in an unshaded position. These pats were constructed by putting one litre of dung on top of a wire grid (25 x 25 cm, 1 cm^2 mesh size) placed on the ground. A second grid was placed on this dung and another one-litre allquot was placed on top of this, producing a complete two-litre pat, divided in half. Each day for 10 days three complete pats were removed. The top and bottom layer were sealed in separate bins and the top 2 cm of the soil beneath the pat was collected in a third bin. Pats were collected at about 9:00 a.m. Beetles were extracted from these samples in Berlese funnels. Numbers of each species found in each layer were compared using ANOVA. Microhabitat data collection also yielded successional data when the totals for the strata of each pat were combined, giving daily totals of beetles from three dung pats over a period of 10 days.

4.2.4 Statistical analyses

The effects of site and strata on the abundance of each species were examined separately using a Kruskall-Wallace one-way analysis of variance by ranks. The effect of time of year (month) and succession (day) on the abundance of each species

was compared in the same way. The mean day of occurrence in the succession, Successional Mean Occurrence (SMO) of each species, was calculated from the following formula:

$$SMO = \sum_{i=1}^{n} p_i (t_i - t_{i-1})\, t_i \Big/ \sum_{i=1}^{n} p_i (t_i - t_{i-1})$$

where p_i is the number of individuals extracted from pat of age t_i (in days) and n is the number of "sampling points' along the succession (in this case, 10). This mean occurrence was also calculated for the month of year and the site for each of the species (Hanski, 1980b).

The niche width (Hanski and Koskela, 1978) for each parameter above was calculated for each species from the following form of the Shannon-Wiener index (SWI).

$$H' = \frac{n \log_n - \sum_{i=1}^{k} f_i \log f_i}{n}$$

Here, k is the number of categories, n is the sample size and f_i is the number of observations in category i (Zar, 1984). From these data a season habitat occurrence diagram (Hanski and Koskela, 1979) was constructed to illustrate the degree of overlap of preferred habitat and season in the three study species, using the SMO as the central point on a niche axis, and the SWI as the spread of a species along that axis.

To examine the interaction of season and site on the local abundance of the beetles, monthly catch data per species were combined for the dry season (April - September), and combined for the wet season (October - March). A log-linear model (Statgraphics 4.0) was fitted to these data. Differences at the 95% confidence interval were noted.

Because pats of the same size were chosen in the field, absolute numbers of beetles, rather than beetle density was used to calculate levels of aggregation (Sevenster, 1996). Coexistence was analysed using measures of intraspecific and interspecific aggregation (Ives, 1991). Intraspecific aggregation J_A, is defined as

$$J_A = V_A/N^2 - 1/N$$

where V_A is the sample variance for species A. N is the mean number of species A per sample. The significance of departure of J_A from zero can be tested using the Chi square dispersion test (Pielou, 1977). Interspecific aggregation C_A is defined as

$$C_A = COV_{A,B}/NM$$

where $C_{A,B}$ is the covariance between species A and species B, N and M are the mean numbers of beetles per sample. The significance of interspecific aggregation can be tested using Spearman rank correlation.

4.3 Results

4.3.1 Continental distribution

Figures 1 - 3 illustrate the continental distribution of the three study species derived from the material examined. *P. incognitus* distribution (Fig. 1) is drawn from 28 separate localities (details are set out in Appendix, Table 1). This species appears to be associated with high altitudes in East Africa, and with moderate altitudes at the southern end of its distribution.

P. labdanus (P. maskinius) (Fig. 2), was recorded from 27 localities (Appendix; Table 2) and has a wider distribution than *P. incognitus*, overlapping with *P. incognitus* in the Kenyan highlands, but occurring in the Ethiopian highlands in the north. In the southern part of its distribution, there is overlap again on the eastern side of the continent, but the species has also been recorded from Angola and Namibia in the west.

From its occurrence in museum collections, *P. sanamus* appears to be the most common of the three species, with 48 recorded localities (Fig. 3; Appendix; Table 3). This matches its relative abundance in local samples. At the northern end of its distribution it has been recorded from one specimen from Nigeria, West Africa, and from Kenya and Tanzania in the east. In the south it is widespread, overlapping with the other species but is absent from samples from the Drakensberg.

Figure 1. The recorded distribution of *Philonthus incognitus*.

Figure 2. The recorded distribution of *Philonthus labdanus*.

Figure 3. The recorded distribution of *Philonthus sanamus*.

4.3.2 Macrohabitat association

Although *P. sanamus* dominated the beetle catch at all sites, the other two species show clear associations with a particular site (Fig. 4.). *P. incognitus*, despite being caught in low numbers, is significantly more abundant at Innisfree, the highest elevation site (KW = 24.63; P < 0.001). *P. labdanus* was significantly abundant at the intermediate site, Cluny Farm (KW = 14.22;. P = 0.0001). *P. sanamus* was most abundant at Boukenhoutskloof, the lowest field site, and least abundant at the highest site, Innisfree, but these differences are not significant (KW = 0.18; P = 0.9113).

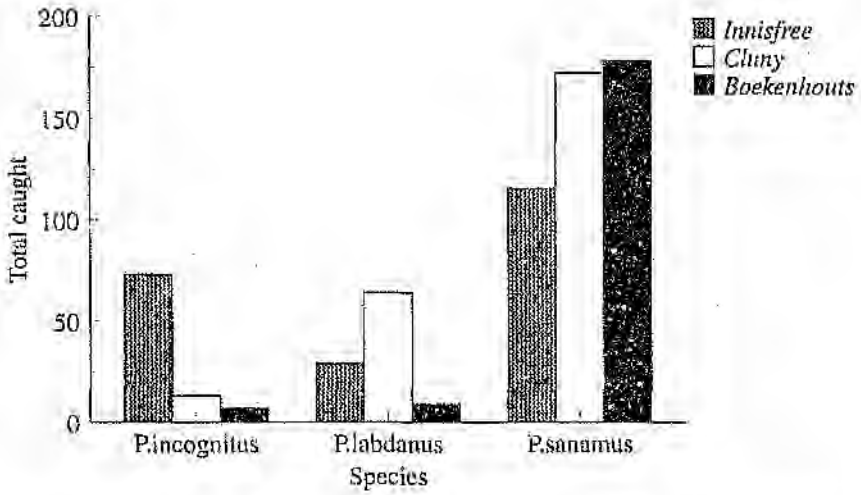


Figure 4. Total catches of three species of *Philonthus* at three different sites for the period March 1990 to March 1991. (See text, Chapt. 2, for description of sites)

4.3.3 Microhabitat selection

Beetles were extracted from all three strata of dung pats. Although all species were most often found in the top or middle stratum, no significant association with any particular stratum was found (Fig. 5; Table 1). *P. sanamus* was again the most abundant of the three species.

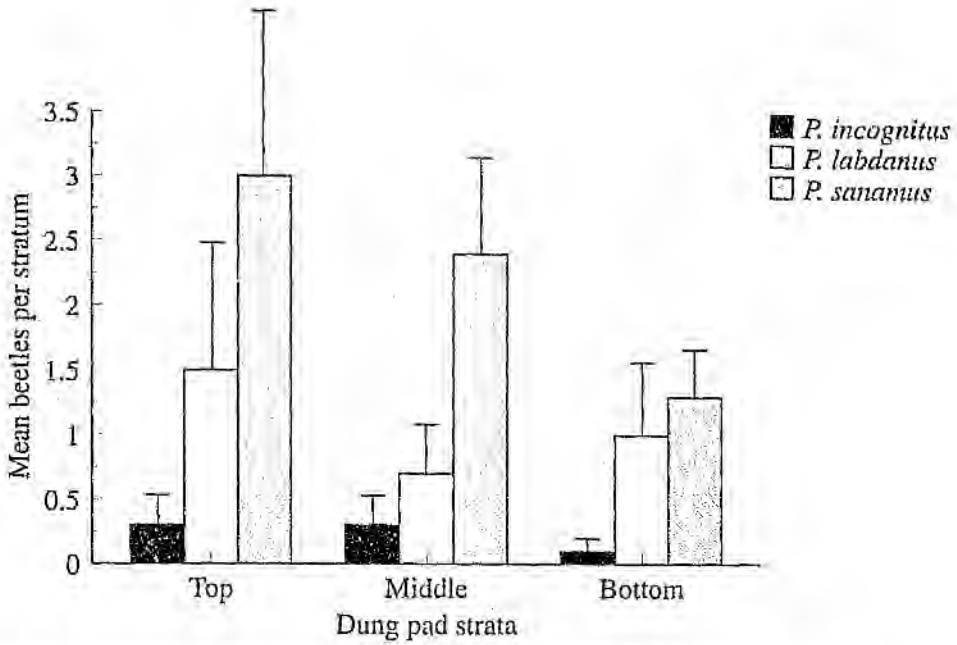


Figure 5. Abundance of three species of *Philonthus* extracted from different strata of dung pats. (Error bars = 1SE)

Table 1. Test statistics for Kruskal-Wallace one-way analysis of variance by ranks of daily totals of beetle species extracted from different dung pat strata. Testing for significant abundance of a species in one stratum of the dung.

Species	K-W Test statistic	P Value
P. incognitus	0.2776	0.8703
P. labdanus	0.1679	0.9194
P. sananus	2.514	0.2844

4.3.4 Seasonal distribution

Each species showed fluctuating abundance through the year. *P. incognitus* appeared in large numbers in February 1991 at Innisfree (Fig. 6a), with a preceding small peak in September to December 1990. The other sites showed a somewhat similar pattern but with generally lower numbers of this species. When totals from all sites are pooled there is little seasonal fluctuation in numbers, except for a significant peak in February (KW 38.58; P = 0.000).

P. labdanus shows a peak in abundance in April at Innisfree (Fig. 6a). There is a second peak in January and February. This pattern is repeated at Cluny (Fig. 6b). Pooled site data give a significant April total (KW = 32.93; P < 0.001).

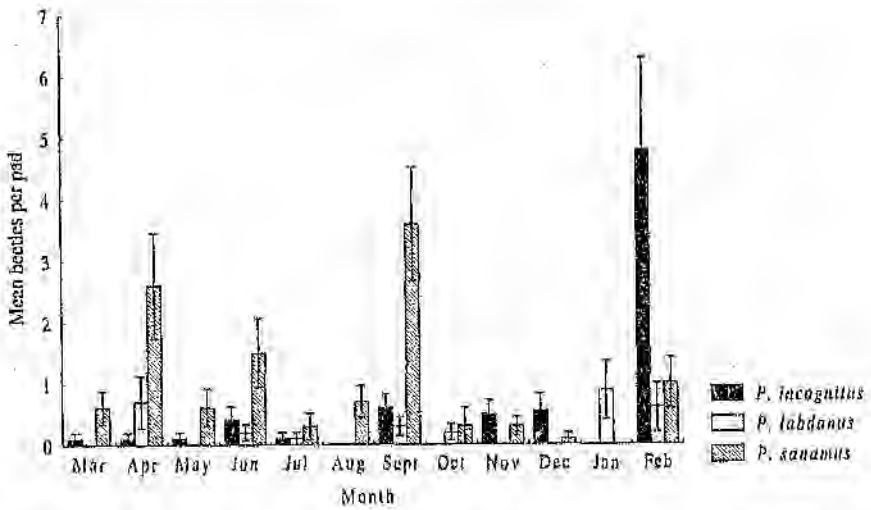


Figure 6a. Seasonal abundance of three species of *Philonthus* at Innisfree farm. (Error bars = 1SE).

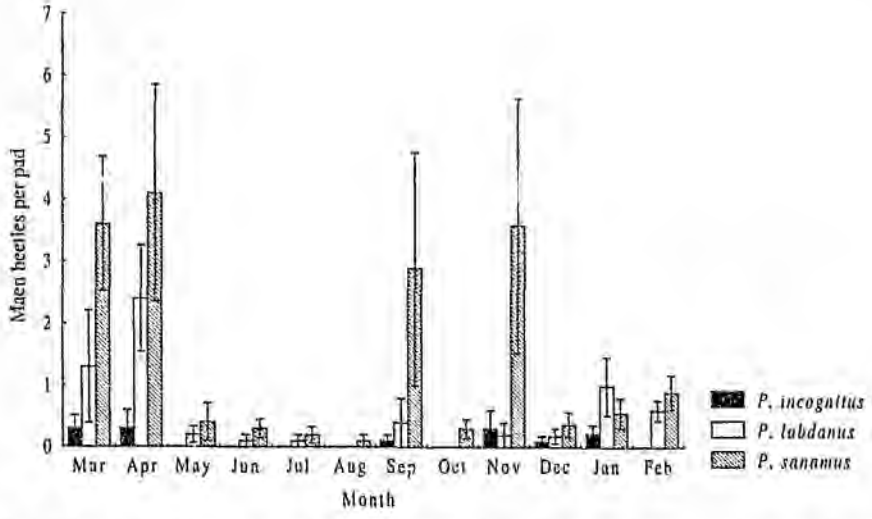


Figure 6b. Seasonal abundance of three species of *Philonthus* at Cluny farm. (Error bars = 1SE).

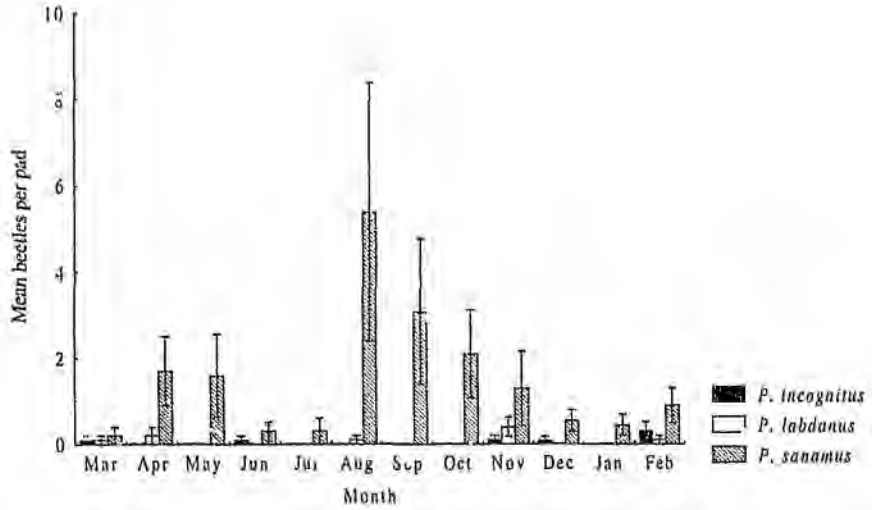


Figure 6c. Seasonal abundance of three species of *Philonthus* at Boekenhoutskloof farm. (Error bars = 1SE).

P. sanamus shows different peaks of abundance dependent on the site. At Innisfree numbers peak in April and September (Fig. 6a), Cluny shows a similar pattern (Fig. 6b), but at Boukenhoutskloof the main peak of abundance is in August. However, when the site totals are pooled, April and September are again the months of significantly large catches (KW = 32.93; P < 0.001).

4.3.5 Succession

The three species arrive at dung in a clear pattern (Fig. 7). All occur from day one and are gone by day seven. *P. incognitus* reaches maximum numbers on day three (KW = 21.89; P = 0.009), *P. labdanus* peaks at day four (KW = 31.62; P < 0.001) as does *P. sanamus* (KW = 42.39; P < 0.001).

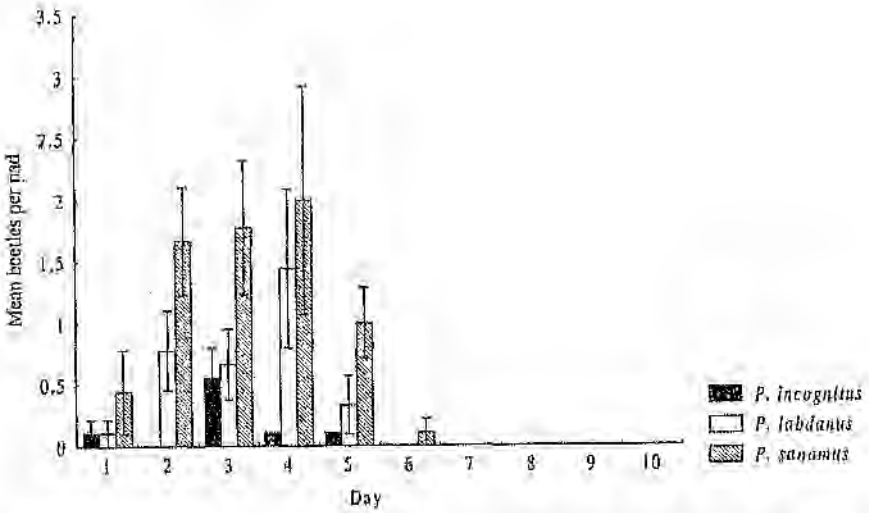


Figure 7. Successional occurrence of three species of *Philonthus* in dung pats. (Error bars = 1SE)

4.3.6 Season and site

Because of the apparent shift of seasonal peaks in abundance of *P. sanamus* at different sites the two factors were combined into a log-linear model to test for interactions between them at the 95% confidence intervals. The interactions that were found to be significant are as follows:

P. incognitus numbers were lower at Boukenhoutskloof and higher at Innisfree than predicted. *P. labdanus* totals were lower at Boukenhoutskloof and higher at Cluny than predicted. *P. sanamus* abundance at Boukenhoutskloof was higher than predicted and lower at Innisfree. This supports the notion of a preferred site for each species gained from earlier analysis.

The effects of season showed *P. incognitus* numbers to be significantly high in the wet season (months April to September), and significantly low in the dry season (months October to March). *P. sanamus* revealed the opposite association, with no effect for *P. labdanus*.

The combined effects of site and season only yielded significant results for *P sanamus*, which was more abundant at Innisfree in the dry season and less in the wet season than predicted by the model. At Cluny, the opposite result was found, low in abundance in the dry season and higher in the wet season.

The succession habitat occurrence plot of SMO and SWI (Fig. 8) and data for seasonal occurrence (Table 2) agree with the preceding analysis in associating each species with a particular site. Seasonal mean occurrence (SMO) places *P. incognitus* and *P. labdanus* at the start of the dry season, but with a seasonal niche width extending over nine months of the year. *P. sanamus* appears in the middle of the year, in the middle of the dry season but extends over ten months of the year.

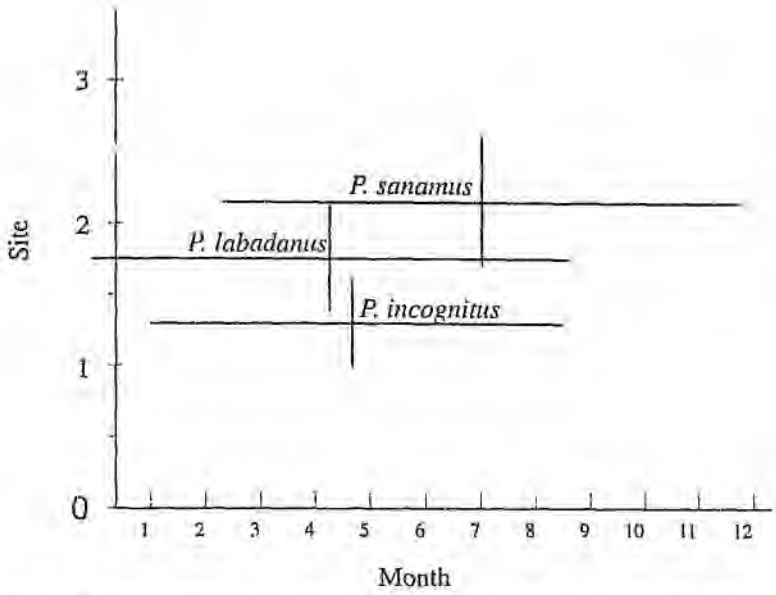


Figure 8. Season habitat occurrence diagram illustrating the degree of overlap between three species of *Philonthus* in seasonal and habitat preference. Site 1 = Innisfree; site 2 = Cluny; site 3 = Boekenhoutskloof. (SMO after Hanski, 1980b and SWI after Hanski & Koskela, 1978)

Table 2. Successional Mean Occurrence (SMO) and niche width (SWI, Shannon Wiener Index) for three species of *Philonthus* collected at three different sites over a twelve month period

	P. incognitus	*P. labdanus*	*P. sanamus*
SMO_{month}	4.8947	4.7843	7.8440
SWI_{month}	0.6909	0.8715	0.9702
SMO_{season}	0.1200	0.4444	0.8684
SWI_{season}	0.2134	0.3003	0.2851

4.3.7 Co-occurrence

Each species showed some degree of positive intraspecific aggregation at all the sites sampled (Tables 3, 4 & 5). Where numbers of beetles caught were large enough to make a calculation of *J*, up to 66.6% of the samples showed significant positive aggregation, and no negative values of *J* were found to be significantly different to zero. Positive interspecific aggregation was found less frequently, but occurred at all the sites and between most combinations of species (Tables 6, 7 & 8), and where numbers were great enough to calculate *C*, between 6.6% and 21% of the samples showed significant positive aggregation, and no negative values of *C* were significantly different from zero.

Table 3a. Intraspecific aggregation of *Philonthus* species in dung pats at Innisfree farm. *J* = Ives (1991) measure of intraspecific aggregation. Probability of *J* being different from zero based on χ^2 index of dispersion with n-1 d.f.. - = frequency of species too small for calculation.

Site 1	*Philonthus incognitus*			*Philonthus labdanus*			*Philonthus sanamus*		
Month	J%	χ^2	P<	J%	χ^2	P<	J%	χ^2	P<
1	-	-	-	125.0	19.00	0.02	-	-	-
2	520.00	34.13	0.001	200.0	21.00	0.01	44.0	13.40	NS
3	-	-	-	-	-	-	0.0	9.00	NS
4	-	-	-	157.0	20.00	0.02	44.0	20.38	0.01
5	-	-	-	-	-	-	50.0	12.00	NS
6	13.0	9.5	NS	-	-	-	44.0	15.60	0.05
7	-	-	-	-	-	-	100.0	12.00	NS
8	-	-	-	-	-	-	-27.0	7.14	NS
9	-50.0	6.00	NS	-	-	-	19.0	16.00	0.05
10	-	-	-	-	-	-	500.0	24.00	0.01
11	-27.0	7.6	NS	-	-	-	-	-	-
12	50.0	12.00	NS	-	-	-	-	-	-

Table 3b. Intraspecific aggregation of *Philonthus* species in dung pats at Cluny farm.

Site 2	*Philonthus incognitus*			*Philonthus labdanus*			*Philonthus sanamus*		
Month	*J*%	χ^2	P<	*J*%	χ^2	P<	*J*%	χ^2	P<
1	-100.0	7.00	NS	44.0	13.4	NS	-28.0	7.60	NS
2	-	-	-	-	-	-	-33.0	6.00	NS
3	100.00	12.00	NS	315.0	50	0.001	38.0	12.50	0.01
4	500.00	24.00	0.0	56	22.5	0.01	115.0	56.24	0.001
5	-	-	-	-	-	-	238.0	18.5	0.02
6	-	-	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-
9	-	-	-	575.0	32.00	0.001	305.0	97.31	0.001
10	-	-	-	350.00	16.00	0.05	-	-	-
11	500.00	24.00	0.01	350.00	16.00	0.05	232.0	92.5	0.001
12	-	-	-	-	-	-	25.0	11	NS

Table 3c. Intraspecific aggregation of *Philonthus* species in dung pats at Boukenhoutskloof farm.

Site 3	*Philonthus incognitus*			*Philonthus labdanus*			*Philonthus sanamus*		
Month	*J*%	χ^2	P<	*J*%	χ^2	P<	*J*%	χ^2	P<
1	-	-	-	-	-	-	13.0	9.5	NS
2	100.0	12.00	NS	-	-	-	56.0	14.00	NS
3	-	-	-	-	-	-	350.0	16.00	0.05
4	-	-	-	350.0	16.00	0.05	118.0	29.06	0.001
5	-	-	-	-	-	-	230.0	45.38	0.001
6	-	-	-	-	-	-	100.0	12.00	NS
7	-	-	-	-	-	-	500.0	24.00	0.01
8	-	-	-	-	-	-	224.0	130.0	0.001
9	-	-	-	-	-	-	205.0	72.65	0.001
10	-	-	-	-	-	-	145.0	39.43	0.001
11	-	-	-	13.0	9.50	NS	283.0	45.85	0.001
12	-	-	-	-	-		13	9.50	NS

Table 4a Interspecific aggregation of *Philonthus* species in dung pats at Innisfree farm. C = Ives (1991) measure of interspecific aggregation. Probability of C being different from zero based on Spearman rank correlation coefficients (r_s). - = frequency of species too small for calculation.

Site 1	*P. incognitus* & *P. labdanus*			*P. labdanus* & *P. sanamus*			*P. sanamus* & *P. incognitus*		
Month	C%	r_s	P<	C%	r_s	P<	C%	r_s	P<
1	-	-	-	-	-	-	-	-	-
2	28.1	0.261	NS	65.0	0.314	NS	66.9	0.800	0.02
3	-	-	-	-	-	-	-	-	NS
4	28.6	0.325	NS	97.8	0.615	NS	38.5	0.142	NS
5	-	-	-	-	-	-	50.0	0.306	NS
6	-	-	-	50.0	0.615	NS	65.0	0.419	NS
7	800	1.00	0.001	500.0	0.750	0.05	500.0	0.750	0.05
8	-	-	-	-	-	-	-	-	-
9	0.0	0.05	NS	-25.0	-0.322	NS	25.0	0.400	NS
10	-	-	-	-	-	-	-	-	-
11	-	-	-	-	-	-	20.0	0.240	NS
12	-	-	-	-	-	-	-	-	-

Table 4b. Interspecific aggregation of *Philonthus* species in dung pats at Cluny farm.

Site 2	*P. incognitus* & *P. labdanus*			*P. labdanus* & *P. sanamus*			*P. sanamus* & *P. incognitus*		
Month	C%	r_s	P<	C%	r_s	P<	C%	r_s	P<
1	-	-	-	44.0	0.373	NS	-	-	-
2	-	-	-	0.0	0.00	NS	-	-	-
3	315.4	0.380	NS	90.4	0.587	NS	100.0	0.589	NS
4	125.0	0.139	NS	98.5	0.880	0.005	9.8	0.138	NS
5	-	-	-	350.0	0.992	0.001	-	-	-
6	-	-	-	200.0	0.500	NS	-	-	-
7	-	-	-	350.0	0.661	NS	-	-	-
8	-	-	-	-	-	-	-	-	-
9	-	-	-	458.0	0.603	NS	-69.0	0.226	NS
10	-	-	-	-	-	-	-	-	-
11	800.0	1.0	0.001	400.0	0.600	NS	400.0	0.600	NS
12	-	-	-	125.0	0.409	NS	-	-	-

Table 4c. Interspecific aggregation of *Philonthus* species in dung pats at Boukenhoutskloof farm.

Site 3	*P. incognitus* & *P. labdanus*			*P. labdanus* & *P. sanamus*			*P. sanamus* & *P. incognitus*		
Month	C%	r_s	P<	C%	r_s	P<	C%	r_s	P<
1	-	-	-	-	-	-	-	-	-
2	-	-	-	0.00	0.146	NS	-33.0	-0.121	NS
3	800.0	1.0	0.001	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	-
8	-	-	-	8.30	0.072	NS	-	-	-
9	-	-	-	-	-	-	-	-	-
10	-	-	-		-	-	-	-	-
11	350.0	0.655	NS	211.3	0.044	NS	523.1	0.600	NS
12	-	-	-	125.0	0.409	NS	-	-	-

4.4 Discussion

Across the continent, *P. incognitus* shows a typical north east highland to southern lowland distribution. *P. labdanus* also fits the East African to southern African broad distribution described by Davis and Dewhurst (1993), just extending north into the tropical subregion demarcated by Endrödy-Younga (1978). It is absent from the south-western zone. *P. sanamus* has the broadest distribution of the three species, occurring in tropical regions in the north, in the south-western zone in the south as well as the Cape and Transvaal Highveld transitional area (Endrödy-Younga, 1978)

Distribution maps of this nature have many drawbacks because of the low numbers of records involved, and the exact identity of specimens may be in question. Tottenham (1955), for instance, questioned the identity of the few specimens under the name *P. incognitus* in the BMNH (London) collection, and frequently mistakes can occur on locality labels. But the major shortcoming of such maps is that the absence of a species from a particular site proves little or nothing. Nevertheless, it is still valuable to see where animals do occur, and look for patterns in their distribution. What conclusions can be drawn from these figures are that *P. incognitus* appears to be associated with high elevations or cooler areas. *P. labdanus* is also found in these areas, but also in more tropical sites. *P. sanamus* has the widest distribution, extending through tropical and sub-tropical areas, and if the single locality label from Nigeria is correct, could be described as Pan-African. All three species overlap completely in their ranges, and if the relative numbers of specimens in the collections studied are an indication of abundance in the field, then *P. sanamus* is the most abundant of the three species.

On a local scale, all species were found at all sites but their relative abundance changed with altitude and the three species show clear associations with sites of different elevations. This matches the picture gained from their continental ranges.

P. incognitus is most abundant at Innisfree, the highest and coolest site, and most restricted in its distribution. *P. labdanus* is most abundant at Cluny farm, the intermediate site, and *P. sanamus* is most abundant at the lowest, warmest site and is dominant in numbers across all the local sites.

The presence of one species in an area clearly does not preclude the other species and it appears that their distributions may be influenced more by the environment than heterospecifics. This environmental influence may be the effect of temperature caused by altitude, and fits the prediction that *P. incognitus* and *P. labdanus* are cool adapted species and *P. sanamus* is more of a temperature generalist. Small differences in altitude (75 - 410m) have been found to influence the distribution of Scarabaeidae in Europe (Martin-Piera and Lobo, 1992; 1993) and Africa (Davis, 1990; Davis and Dewhurst, 1993), and inevitably this must be reflected in the physiology of the beetles, as has been found in other scarabs (Chown *et al.*, 1995).

From 256 cattle dung pats, Davis *et al.* (1988) extracted a total of 71 *P. sanamus* specimens (0.27 beetles/pat), which indicates the low numbers with which *Philonthus* species occur in the dung environment. A patchy distribution further compounds the problem of generating enough samples for statistical analysis. This appears to be a common problem with most investigations of arthropods associated with patchy ephemeral habitats (Laurence, 1956; Valiela, 1974; Piñero, 1997), and includes scarabs (Giller and Doube, 1994; Lumaret and Iborra, 1996), flies (Papp, 1970, 1993), and mites (Camerik, pers. com.). This large fluctuation in numbers was reflected in the data collected in this study. Nevertheless, 93 *P. incognitus*, 103 *P. labdanus* and 468 *P. sanamus* were extracted from 324 pats in the macrohabitat study (*P. sanamus* = 1.44 beetles /pat).

Hanski and Koskela (1979) concluded that macrohabitat was more important than season in separating temperate predatory species. In contrast, Davis *et al.*(1988) found few significant macrohabitat associations regarding soil type and locality

amongst 31 species of predatory staphylinids in four contrasting subtropical habitats. All of these sites were within a 15 x 30 km area in Zululand at a similar altitude. Habitats in the present study were markedly alike in appearance, usage, shade and ground cover, but being more widely spaced, they differed primarily in altitude and therefore climate. As predicted, the three *Philonthus* species show strong associations with a particular site.

Subtropical beetle assemblages generally show great overlap between species' activity periods (Peck and Forsyth, 1982; Janzen, 1983), in contrast to the well spaced seasonal activity that is seen in temperate beetle communities (Holter, 1982). There is a broad seasonal overlap between the species studied here and this is echoed in the successional overlap found. All three *Spatulanthus* species occurred throughout the year to lesser and greater degrees depending on the site. Strict seasonality was not apparent, but peaks in abundance during spring and autumn can be seen. Davis *et al.* (1988) found a similar pattern for *P. sanamus* in Zululand in the tropical subregion, in contrast to Hanski (1980b), who recorded a unimodal seasonal occurrence for northern temperate staphylinids. Importantly, large-scale dung removal by large scarabs does not occur at higher latitudes. Bimodal seasonal abundance at the end and beginning of the dry season in the southern African region, might be a tactic for avoiding disturbance by dung-burying scarabs which can be detrimental to staphylinid dung fauna (Roth, 1983). Conversely, staphylinids need dung penetrations by other beetles to gain access to the pat interior, but this might be provided by Aphodiinae and Hydrophilidae which are active throughout the year, (Davis 1996b). Boukenhoutskloof was the only one of the sites in this study with a large population of scarabs, and the peak in numbers of *P. sanamus* in August may reflect an avoidance of their activity.

Spatial processes are often invoked as an alternative means of species avoiding interspecific competition. Species may coexist and survive competition, either due to good dispersal or good competitive abilities, and these are based on the existence

of spatial and temporal refugia (Hanski and Cambefort, 1991a).
Variance/covariance models (Hanski, 1991) use aggregation as a basis to explain coexistence even if no resource partitioning in the traditional sense is seen. If the superior competitor is highly aggregated then this leaves more low density or empty sites in which the inferior species can breed. These are known as probability refuges and experimental data supports their existence (Shorrocks and Rosewell, 1987; Ives, 1991; Sevenster and van Alphen, 1996).

From the data presented, clear spatial and temporal overlap exists between the three species of beetles studied, so that resource partitioning in terms of habitat use has not been shown to occur. There was some evidence of interspecific aggregation amongst some species pairs on some occasions, but there was no evidence of negative species associations between species pairs. Intraspecific aggregation in insects within patchy ephemeral habitats is well known, and has been observed in temperate (Hanski, 1980c; Holter, 1982) , subtropical (Kohlman, 1991) and tropical dung beetles (Janzen, 1983; Giller and Doube, 1994). The underlying mechanism for this aggregation is not clear and could be any one of the following. Resource quality may differ between dung pats. This was not controlled in these experiments, but most other experimental studies mentioned standardised pat quality and still found patchy insect distributions. Pheromones may cause aggregation of beetles in pats (Tribe, 1975), especially where beetle numbers are low (Holter, 1982), as they are in these species. Crowson (1981) has suggested that the osmeterium (Chapter 2) of *Philonthus* may serve some purpose for attraction or aggregation of the species. But it must be borne in mind that most animals, regardless of their habitat and ecology are more or less aggregated at most spatial scales (Taylor *et al*., 1978). This is to be expected as they have common needs and have to encounter each other to reproduce.

All three species examined here show degrees of intraspecific aggregation which is contrary to theoretical expectations (Ives, 1991), because *P. incognitus*, which at this

stage has to be considered the inferior competitor being very low in abundance, is not randomly distributed between samples. In addition, the absence of negative interspecific associations between species suggests that resources presented by the dung habitat may not be limiting for these species, and that competition may be weak or infrequent. Valiela (1969b) calculated feeding rates for predatory beetles and was able to conclude that predators are not food limited in communities of dung invertebrates (Valiela, 1974). Therefore it is assumed that some other factor is influencing the distribution of the study species. The factors that will be examined in further chapters are the effects of temperature on development and survival, the life history strategies of the species, and the effect of competition on reproduction and survival in a limited resource environment.

CHAPTER FIVE.

THERMAL BIOLOGY OF *P. incognitus*, *P. labdanus* AND *P. sanamus*

5.1 Introduction

The previous chapters have shown *P. incognitus*, *P. labdanus* and *P. sanamus* to be closely associated with each other and to form a definite subset of the dung insect community. They appear to coexist closely at all scales investigated, but have differences in abundance and distribution that could possibly be correlated with altitude and latitude. Distribution maps and macrohabitat associations of these beetles suggest that the difference in their ranges is influenced by environmental temperature (Chapter 4). *P. sanamus* has been collected from a broad range of sites, while *P. incognitus* and *P. labdanus* appear to be more restricted to high altitude sites at lower latitudes. Altitude is directly correlated with ambient temperature, and altitudinal clines are paralleled by latitudinal clines (Partridge and Coyne, 1997, Jay-Robert *et al.*, 1997). Ecologically and phylogenetically closely related species have been found to have mutually exclusive altitudinal ranges more frequently than expected by chance (Jay-Robert *et al.*, 1997). Therefore, if the thermal biology of such species has a limiting influence on their distribution, then one would expect to find differences in the thermal biology of the beetles that correspond to their large scale distributions (Martin-Pierra and Lobo, 1992). In this case one would predict that *P. sanamus* should show adaptation to warmer habitats than *P. incognitus* or *P. labdanus*. Chown *et al.*, (1995), have used thermal biology and desiccation resistance in a similar fashion to explain the macrohabitat selection and continental distribution of a flightless scarabaeid dung beetle.

Habitat selection has physiological consequences for any organism and therefore this selection is ecologically important (Huey, 1991). Physiological limitations may totally preclude an animal from occurring in an area. Of all environmental factors influencing life, temperature is generally considered to have the most profound effect on all aspects of the life-cycle of an organism, affecting rates of metabolism, production and mortality (Sibly and Atkinson, 1994). Temperature, and secondarily moisture, are found to be the most important climatic predictors of arthropod distributions (Sutherst and Maywald, 1985). The effects of extreme temperatures, such as heat stress, delimit the occurrence of arthropods in deserts and some low-lying coastal areas, while cold stress is important in temperate climatic regions of southern Africa (Perry *et al.*, 1990).

What is less clear are the constraints on the evolutionary expansion of species ranges, from the abundant genetic variation available in most natural populations (Mongold *et al.*, 1996). If one organism can adapt to live at the poles, then why can't more? (Hutchinson, 1959). One popular explanation is that adaptation to a novel environment will involve a trade-off, such as a reduction in performance in another environment, or other life-history trait. This "sum-zero" effect is widely assumed for a variety of life-history trade-offs, but has little empirical support (Mongold *et al.*, 1996). Such an assumption has also been proposed as a restraining factor on runaway development of secondary sexual characters, and has recently been confirmed by experimental evidence from dung beetles (Roush, 1997). For physiological adaptations, most support has come from the correlation between distribution and thermal characteristics of organisms, of which the latitudinal cline in species diversity is globally, the most striking. However, temperature effects are not always accepted as the underlying cause for these diversity gradients or example, many marine taxa exhibit a pronounced East-West cline in species richness, from an area of high concentration in the Indo-West Pacific (Clarke, 1996). Another alternative explanation argues that global patterns of diversity are the result of the correlation between area and diversity, but in reality this relationship is also

not that straightforward (Rohde , 1997). Southern temperate areas may in fact be more species rich, depending on which taxon is examined (Platnick, 1991). Climate may influence latitudinal diversity though area effects, because some tropical species are found to have both narrower climatic tolerances and small geographical ranges (Stevens, 1989).

There are few cases where temperature can be shown unequivocally to be the factor defining distribution limits, although other factors may be involved in demarcating the perimeter of a species range. Both biotic and abiotic features will create an edge, towards which "sink" populations will reproduce less successfully than central "source" populations (Lawton, 1993). This structure may appear stable over a short, human time-scale, but the fossil and ice core record reveals recent radical climate change that has been likened to a "flickering switch" (Taylor *et al.*, 1993), and suggests that extreme events rather than mean climate may be more important in terms of effect on organisms. Four options are open to an organism in the face of climate change: to move elsewhere, to stay put and cope, to adapt, or to go extinct. It appears that climate change will probably outrun evolution (Clarke, 1996), and that organisms are more likely to track favourable habitats, but as individual species and not as communities (Coope, 1979). This both weakens the support for equilibrium structured communities, and suggests that abiotic features may be more important than biotic factors such as competition, in structuring communities. The fossil record implies that species do not have the ability to adapt out of trouble, but conflicting empirical data on thermal adaptation in *Drosophila* exist (Mongold *et al.*, 1996).

Each organism is to some extent adapted to its environment. This adaptation is not trivial because it represents a success story going back to its ancestors, and consequently adaptation is assumed to constrain the organism, such that it is caught in a phylogenetic trap. Populations are expected to retain characters from a previous environment (Bartholomew, 1987; Feder, 1987). If the character is thermally

dependent, it can be measured and interpreted, usually in an adaptive context, and compared amongst organisms inhabiting a similar thermal environment, and comparisons of close relatives are considered more likely to reveal adaptations to environmental conditions (Huey, 1987). For insects displaying what appears to be an overlapping climate distribution in a rapidly changing micro-habitat, then temperature dependent rates of development of immature stages would seem to be an appropriate gauge of the relative influences of biotic or abiotic factors on their physiology. In addition, quantifying the lower developmental thresholds and upper thermal limits of the beetles will give some measure of the thermal niche of each species. Lethal temperatures set an ultimate boundary to a thermal niche, and along with physiological optima can be used to define the thermal niche.(Magnusson *et al.*, 1979).

5.1.1 Thermal niche

The concept of thermal niches is well-entrenched, with resource partitioning generally given as the reason for their existence if not origin. Magnusson *et al.*, (1979) argue that temperature can be regarded as an ecological resource equivalent to food, and therefore, while there can be no competition for any particular ambient temperature, the time or space in which an organism can attain optimal heat exchange can be the goal of competing species, and so influence the fitness of a species (Tracy and Christian, 1986).

Most studies of physiological differences between sympatric species have been done on reptiles, amphibians and fish (e.g. Magnusson *et al.*,. 1979). The studies on arthropods (as with reptiles), have centered on animals living in extreme environments such as tenebrionids (Holm and Edney, 1973; Fallaci *et al.*, 1997), ants (Marsh, 1987; Cerda *et al.*, 1997; De Bie and Hewitt 1990). A combination of factors is commonly measured, including behavioural thermoregulation, upper and lower lethal temperature limits, and rarely, metabolic rate (Schultz and Hadley,

1987). These studies generally have examined temporal rather than spatial separation of congeners, concluding that potential competitors have different activity times dictated by their thermal tolerances. Spatial habitat segregation by predatory cicindelids is correlated with different "physiological constraints/adaptations" (Schultz and Hadley, 1987). These authors found differences in the metabolic rates, and upper thermal limits of two sympatric species of tiger beetles occupying different strata of a riverine beach.

There is probably a cost/benefit balance; as in the evolution of many specific traits, between being a broad temperature generalist or a narrow range specialist. The former may be constrained by metabolism biochemistry (Huey and Hertz, 1984), and the latter by external factors like predation or the vagaries of climate (Heinrich, 1993). This will have similar and different implications depending on what stage of the insect's life cycle is being considered.

5.1.2 Larval development

Efficient exploitation of the thermal environment can result in faster growth rates of ectothermic animals (Tracy and Christian, 1986). If metabolism cannot be organised to operate at maximal efficiency over a broad range of temperatures, then insect larvae in general must be under considerable selective pressure to either thermoregulate effectively, or have a temperature-independent metabolism to accelerate growth rate as much as possible to reduce the exposure to predators (Heinrich, 1993). Rapid growth is essential for an insect living in an ephemeral environment such as a dung pat. Therefore the evolution of an optimal developmental temperature is not surprising, nor is the notion that this optimum should be different for species originating in, or adapted to, different habitats. Many species of caterpillars are reported to exhibit behaviours that maintain body temperature at optimal levels for maximum growth rate (Heinrich, 1993). Stam (1997), has show that of three geographical populations of the collembolan

Orchesella cincta, the high latitude population has an elevated metabolic rate, which he assumed allowed completion of development in the shorter growing season.

The relationship between rearing temperature and the rate of development, expressed as the reciprocal of the time taken to complete a particular developmental stage, approximates a straight line between a base temperature of developmental zero (t), below which no development occurs, and (T_o) a temperature "optimum". This technique of calculating rate of development is widely used and validated (Atkinson, 1996). The real curve is sigmoid, as the curve becomes less steep near t and T_o, and survival decreases. In addition, experiments at lower temperatures take a very long time to complete. Because of this, developmental zeroes are often estimated by extrapolation from developmental rates at higher temperatures. While the linear model of development might not be biologically realistic, it gives results that correlate well with more complex non-linear models and is appropriate for comparing developmental rates (Klingenberg and Spence, 1997). Geden (1997) compared a linear regression degree day model with a biophysical model and found neither to be a superior predictor of developmental times. Wagner *et al.*, (1984) reviewed methods of modelling insect development rates and noted that linear regression models of development were valid over intermediate temperatures; those lying between the upper and lower developmental thresholds. Pilot studies with *P. sanum.is* indicated these to be below 12 °C and above 35 °C respectively. Despite the apparent drawbacks of the linear model, it is still widely used because it is simple and it works. (Balstisti and Cescatti 1994; Geden, 1997).

5.1.3 Lethal temperatures

Insect larvae can be active over a wide range of body temperatures. Heinrich (1993) associates this broad thermal tolerance with them having a few thermoregulatory options; whereas eggs and pupae have none. Their temperatures are a function of their environment which the adults or larvae have chosen for them. The adults at the

very least would be expected to avoid extremes of heat or cold, which must be true of the study animals as they are too small to be endothermic (McNab, 1983), or to have enough water reserves to use evaporative cooling to reduce body temperature. Evaporative cooling may allow survival to acute heat exposure for short periods, and may take a variety of forms such as increased ventilation (tenebrionids), extrusion of genitalia, or opening of the spiracles (May 1985). Aphids, although very small, have been shown to stilt, and then extrude and withdraw honeydew from the anus to change the rate of heat exchange, but this is exceptional behaviour as the aphids have access to a copious supply of fluid. Although adult *Philonthus* spend their time at dung pats inside the dung, which has large amounts of free liquid available, the surrounding air will be saturated with water vapour, removing the gradient needed for evaporative cooling. Therefore avoidance of temperature extremes is probably the only thermoregulatory strategy open to these beetles.

Avoidance of lethal temperatures rather than tolerance of extremes must be of primary importance for most insects, as the onset of heat torpor precludes any action by the animal to prevent further heating. Behavioural thermoregulation studies usually involve some measure of the extremes of temperature that can be tolerated by the insect, either as the upper lethal temperature (LT_{50}), (Mitchell *et al.*, 1993), or critical thermal maxima (CT_{Max}), (De Bie and Hewitt 1990; Klok and Chown, 1997). These methods have been used to describe the ecological limits of the insect's thermal niche (Marsh, 1985). CT_{Max} is usually determined by heating the insect at a rate of 1 °C/minute until heat torpor develops. Heat torpor is loosely defined as loss of motor control, inability to right, or inability to move away from a lethal heat source. There is no hard and fast procedure for applying these tests as they have been performed from between minutes to days after heat exposure.

LT_{50} appears to be a more precise measure of lethal temperature, defined as the temperature at which 50% of the sample population die. But the time spent at that temperature is obviously of prime importance and is usually set by the investigator

based on ecological observations. The precise definition of death is problematic in insects, and whether it should be recorded immediately after heat exposure or some time afterwards (Mitchell *et al.*, 1993).

CT_{Max} is considered to take less time and animals to measure than LT_{50} but has drawbacks in establishing exactly when heat torpor is reached, and that flying insects can escape the heated substrate by taking to the air. Heating the air instead may prove too vigorous for small creatures such as staphylinid beetles, and does not necessarily heat the substrate evenly. The LT_{50} method was chosen for these trials as it appeared to offer more precision in the collection of data and calculation of temperature limits for comparison between species. CT_{Max} may be more useful when looking at actual field temperatures that may be encountered by the animals.

5.1.4 Acclimation

Temperature acclimation has been shown in a variety of organisms from yeasts to mammals (Yocum and Denlinger, 1994) and can change with age, sex, state of hydration or feeding. Surviving a thermal stress depends in part on the individual organism's stress history. The upper lethal temperature of an insect can be raised by prior exposure to sub-lethal temperatures (Sømme, 1995). This acclimation effect is widespread among insects and may reflect the change in environmental temperatures as the seasons change. Acclimation can also occur at the population level and therfore justifies careful standardisation of age and physiological state of the animals under test (Cloudsley-Thompson, 1975).

5.2 Methods

Because the thermal history of individual insects and populations has been shown to have a profound consequence on their response to thermal stress (Mitchell *et al.*, 1993; Yocum and Denlinger, 1994), care was taken to eliminate this effect from the

experimental design. All parental stocks of *Philonthus* for these trials were collected from the Cluny field site, therefore any locality influences or the effects of differential acclimation should have been controlled for. The developmental data were generated from F2 progeny of F1 laboratory animals reared at 25 °C, as were the F1 animals used for the lethal temperature experiments.

5.2.1. Effect of temperature on rate of development

To measure the effect of temperature on the rate of development of the immature stages of *P. sanamus*, *P. labdanus* and *P. incognitus*, eggs were collected from approximately 60 pairs of adults (F1) of each species. These adults had been laboratory-reared at 25 °C and were set up on dung and soil at 25 °C, with two pairs per two-litre container (Bearing, Chapter 2). Eggs were gathered every six hours, when the adult *Philonthus* were reset back into the same pots, onto new dung which had been previously frozen and thawed to sterilise it. Thirty eggs of each species were placed on damp filter paper in individual petri-dishes, and put into closed five-litre plastic boxes, at each of the following temperatures: 15, 20, 25 and 30 °C in Labotec Termo-Mat Model 349 low temperature incubators (15, 20, 25 °C) and a low temperature Labcon LTIE incubator (30 °C). Temperature was monitored using copper/costantin thermocouples attached to an MCS EX2 data logger. Thermocouples were calibrated at 0 °C and 50 °C prior to the experiment.

Observations were made every six hours to record changes in developmental stages. Moulting is easily noted as the larva does not eat the head capsule. After 12 days, the observation period was extended to 12 hour intervals. When the third instar was reached, larvae were transferred into 45 ml pots with 30 ml of soil. A 2 cm^3 block of damp sponge was added to each pot to maintain the soil humidity. *Musca domestica* eggs were added as food for the larvae at each observation. Pupation was considered to have begun when the L3 larva disappeared from the soil surface. This

was shown to be a consistent behaviour in pilot trials. Appearance of the newly eclosed adult on the soil surface was recorded as the end of the pupal stage.

Due to space restrictions, *P. sanamus* larvae were reared first, before the other two species, and the average incubator temperatures were slightly different on each occasion. Therefore results were analysed by performing linear regressions on the inverse of the developmental time in hours at each temperature, for each stage of each species. Differences in rates of development were examined by comparing the slopes of the developmental curves for each species by ANCOVA (Rudestat, Lighton, 1994). Lower threshold temperatures were determined by extrapolation of the regression line to zero (Campbell *et al.*, 1974). Lower thermal thresholds (t) for immature stages were calculated from

$$t = -a/b$$

where a = slope and b = intercept of the linear regression. The standard error (SE) of t is approximately

$$SE_t = \bar{y}/b\sqrt{\frac{S^2}{Ny^2}+\left[\frac{SEb}{b}\right]^2}$$

where S^2 is the residual mean square of y, and y is the mean of all the samples expressed as one/time and N is the number of paired observations. The thermal constant k was estimated for each species from 1/b. The standard error of k is approximately

$$SE_K = \frac{SE_t}{b^2}$$

Rates of development for each species were compared by ANCOVA (Rudestat, Lighton, 1994). For direct comparison of each species under different conditions, development times at selected temperatures were determined by interpolation of the developmental curves.

5.2.2 Upper lethal temperature.

To measure upper lethal temperature, beetles of all three species were reared to adult at 25 °C, and fed *ad lib.* Two weeks after emergence, 10 individuals were transferred by pooter into two-litre plastic jars maintained at the experimental temperature. Damp filter paper was placed the floor of the jar, and a moist sponge was suspended from the lid, to maintain humidity close to RH 100%.

Beetles were exposed to the experimental temperatures for one hour, (calculated by averaging the temperature readings for the last 45 minutes of exposure). Air temperature was recorded inside the flask every minute, via a copper constantin thermocouple attached to an MCS EX2 data logger. Mortality was recorded by removing the beetles from the jar and testing their righting reflex. Those beetles which could not right themselves after 15 minutes at 25 °C, were considered to be dead

Results were analysed by linear regression of percent mortality recorded at each experimental temperature, and the curves generated for each species were compared by ANCOVA (Rudestat, Lighton, 1994). LT_{50} was calculated for each species by interpolation of the regression line.

5.3 Results

5.3.1 Development

The developmental curves (Figs 1 - 6) display the differences in rates of development of each species at different temperatures. The rates of development for each species are very similar at all temperatures, but nevertheless are significantly different in some cases. *P. sanamus* has the steepest developmental curve for all stages (Table 1; Fig. 1). This curve is significantly different to both *P. incognitus* and *P. labdanus* for all stages except L1 (Table 2). There is no significant difference between the slopes of the curves for eggs L1 and L2 of *P. incognitus* and *P. labdanus* (Table 1; Figs. 1-6).

Developmental thresholds (t) and thermal constants (K) (Table 1) were calculated for each species from the slopes of their respective developmental curves (Figs 1 - 6). These values can be considered to be significantly different if the slopes of the curves for each species are significantly different (Table 2). These measures of t and K follow a similar specific pattern to the developmental rates, with *P. sanamus* having the highest developmental thresholds, two to three degrees above the other species, and lowest number of degree days required for development. *P. labdanus* has the lowest calculated developmental threshold, about 0.5°C lower than *P. incognitus*.

Table 1. Lower developmental thresholds (t) and thermal constants (K) for immature stages of three species of *Philonthus*.

Species / Stage	Equation	t ± SE (°C)	K ± SE (°D)	r^2
P. incognitus				
Egg	y = -0.01120 + 0.001147x	9.76 ± 0.31	36.3 ± 0.90	0.9394
L1	y = -0.02594 + 0.002444x	10.61 ± 0.46	17.0 ± 0.62	0.8838
L2	y = -0.02045 + 0.001927x	10.61 ± 0.41	21.6 ± 0.67	0.9143
L3	y = -0.01350 + 0.00118x	11.41 ± 0.59	35.2 ± 1.66	0.8297
Pupa	y = -0.00268 + 0.000244x	11.02 ± 0.23	171.1 ±3.14	0.9747
All	y = -0.00159 + 0.000147x	10.86 ± 0.17	283.8 ± 3.82	0.9863
P. labdanus				
Egg	y = -0.00993 + 0.001087x	9.14 ± 0.83	38.3 ± 2.22	0.7395
L1	y = -0.02229 + 0.00225x	9.90 ± 0.52	18.5 ± 0.71	0.871
L2	y = -0.02141 + 0.00199x	10.76 ± 0.45	20.9 ± 0.69	0.9028
L3	y = -0.00916 + 0.000901x	10.16 ± 0.57	46.2 ± 1.9	0.8598
Pupa	y = -0.00211 + 0.000206x	10.23 ± 0.24	202.2 ±3.88	0.9693
All	y = -0.00128 + 0.000127x	10.11 ± 0.16	328.5 ±4.25	0.9861
P. sanamus				
Egg	y = -0.01434 + 0.001241x	11.55 ± 0.12	33.6 ±0.38	0.9854
L1	y = -0.02621 + 0.00237x	11.06 ± 0.31	17.6 ±0.44	0.9346
L2	y = -0.02906 + 0.002491x	11.66 ± 0.43	16.7 ± 0.59	0.8833
L3	y = -0.01392 + 0.001226x	11.35 ± 0.42	34.0 ± 1.17	0.8964
Pupa	y = -0.00343 + 0.000267x	12.86 ± 0.19	156.2 ± 3.05	0.9689
All	y = -0.00200 + 0.000161x	12.41 ± 0.15	258.2 ± 3.87	0.9815

Table 2. Statistical analysis (ANCOVA) of developmental curves for *Philonthus* species. Testing for equality of slope: (change in rate of development).

Stage	Species			F value	Degrees of freedom	P value
	P. incognitus	*P. labdanus*	*P. sanamus*			
Egg	*	*		4.21	(2,324)	0.015
L1	*	*	*	1.48	(2,312)	0.227
L2	*	*		18.518	(2,302)	0.000
L3				15.034	(2,285)	0.000
Pupa				47.354	(2,247)	0.000
All				76.459	(2,245)	0.000

* Denotes those stages in the same row that are not significantly different from each other

Table 3. A comparison of developmental times in days for immature stages of three species of *Philonthus*.

Temperature	Stage	*P. incognitus*	*P. labdanus*	*P. sanamus*
15 °C	Egg	6.9	6.5	9.7
	L1	3.9	3.6	4.5
	L2	4.9	4.9	5.0
	L3	9.8	9.6	9.3
	Pupa	42.5	42.5	72.5
	All	68.5	67.1	99.5
20 °C	Egg	3.5	3.5	4.0
	L1	1.8	1.8	2.0
	L2	2.3	2.3	2.0
	L3	4.1	4.7	3.9
	Pupa	18.9	20.7	21.8
	All	31.0	33.2	34.0
25 °C	Egg	2.4	2.4	2.5
	L1	1.2	1.2	1.3
	L2	1.5	1.5	1.3
	L3	2.6	3.1	2.5
	Pupa	12.2	13.7	12.8
	All	20.1	22.1	20.5
30 °C	Egg	1.8	1.8	1.8
	L1	0.9	0.9	0.9
	L2	1.1	1.1	0.9
	L3	1.9	2.3	1.8
	Pupa	9.0	10.2	9.1
	All	14.8	16.5	14.7

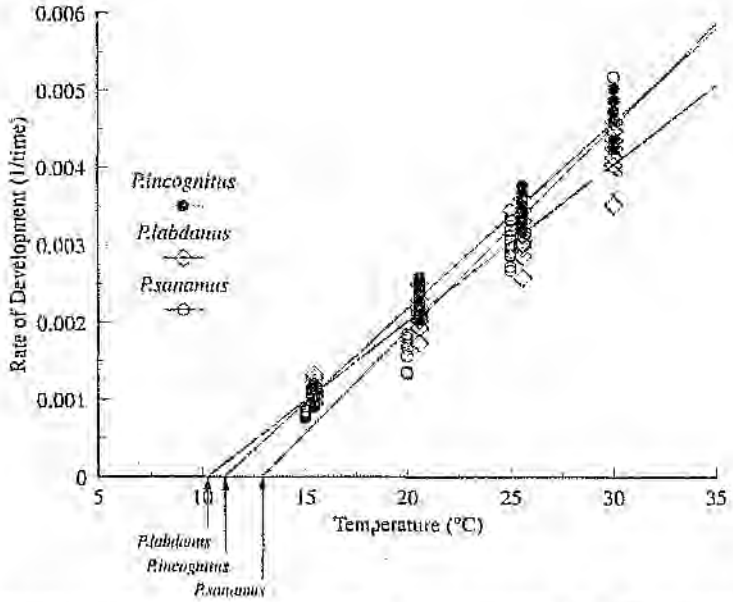


Figure 1. The relationship between temperature and development for all stages (egg to adult) of three species of *Philonthus*.

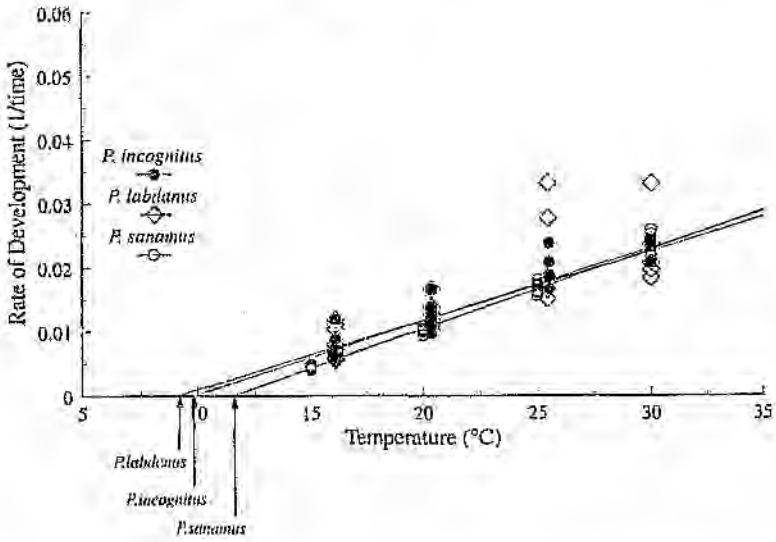


Figure 2. The relationship between temperature and development of the egg stage of three species of *Philonthus*.

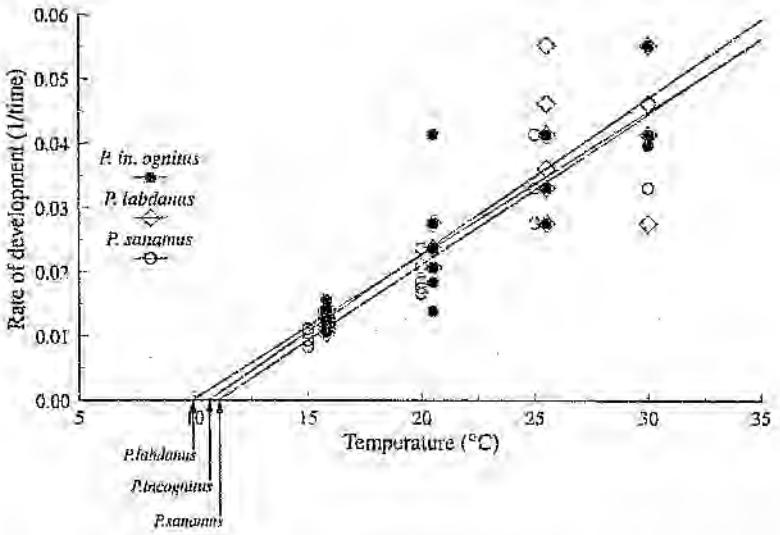


Figure 3. The relationship between temperature and development of the first instar stage of three species of *Philonthus*.

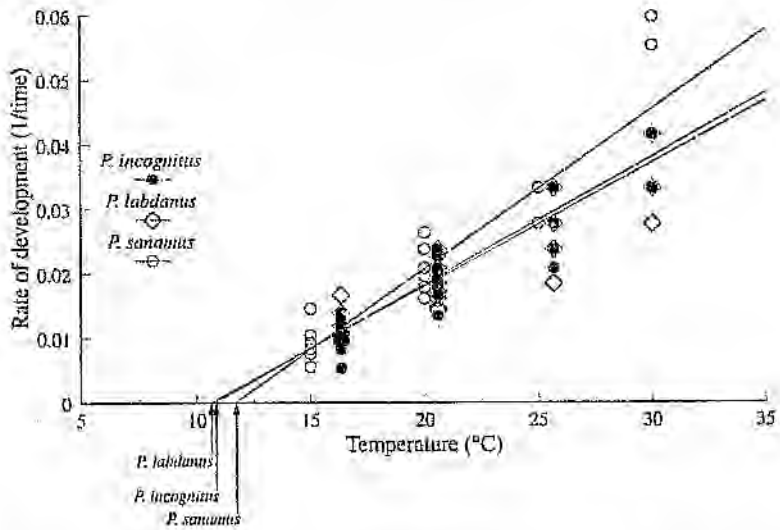


Figure 4. The relationship between temperature and development of the second instar stage of three species of *Philonthus*

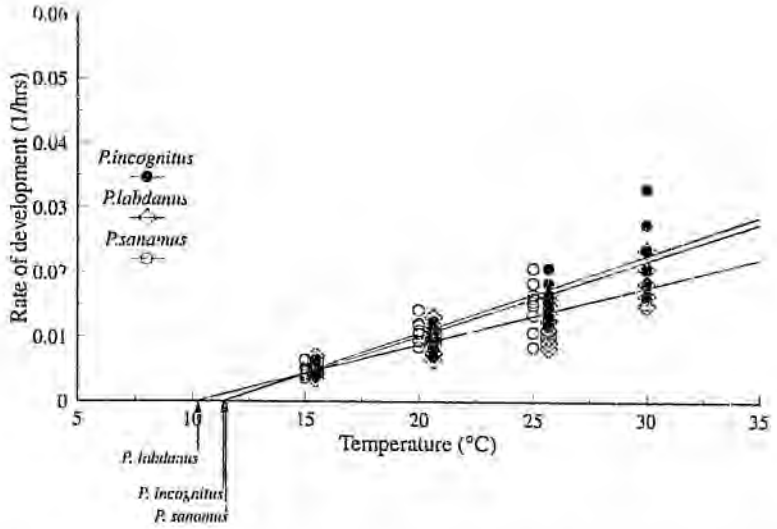


Figure 5. The relationship between temperature and development of the third instar stage of three species of *Philonthus*

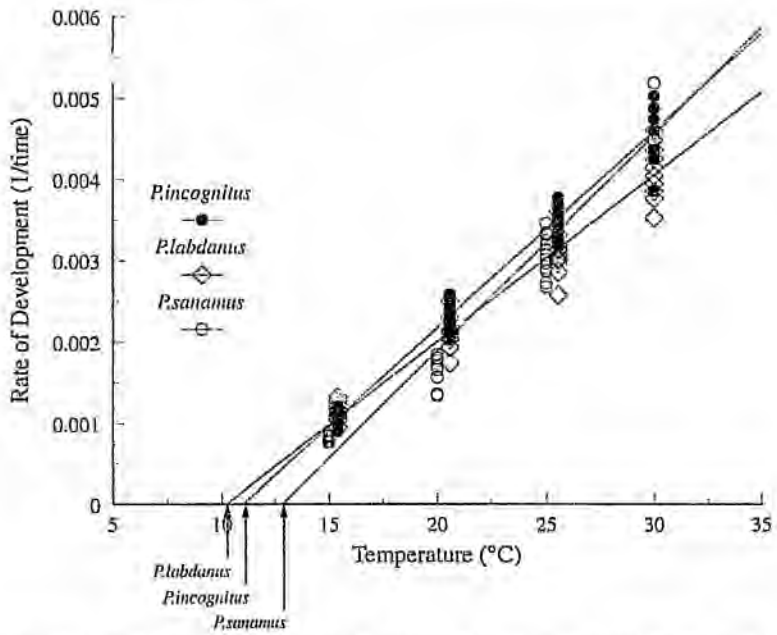


Figure 6. The relationship between temperature and development of the pupal stages of three species of *Philonthus*.

5.3.2 Lethal temperature

Of the study beetles, *P. labdanus* has the lowest LT_{50}, *P. sanamus* has the highest, and *P. incognitus* again fills an intermediate position (Table 3). These differences are significant as the intercepts of the mortality curves are significantly different ($F = 13.9283$, $df = 2,19$, $P = 0.001$]. It is notable that the slopes of these curves are not significantly different from each other ($F = 1.5158$; $df = 2,17$; $P = 0.247$). Therefore, the rate at which the different species succumbed to high temperatures can be considered to be the same.

Table 3. Upper lethal temperatures (LT_{50}) of three *Philonthus* species.

Species	Equation	LT_{50} (°C)	r^2
P. incognitus	y = -1610+40.3x	41.09	0.6528
P. labdanus	y = -2300+58.2x	40.48	0.9327
P. sanamus	y = -1330+32.3x	42.82	0.7286

5.4 Discussion

The rates of development of *P. incognitus*, *P. labdanus* and *P. sanamus* presented here are similar to those determined for other dung-breeding *Philonthus* (Hafez, 1939b; Prins, 1984; Hunter *et al.*, 1986), and those of species found ranging in European agricultural fields (Eghtedar, 1970; Heessen *et al.*, 1982). Therefore, this convergence is more likely to be the result of phylogenetic constraints (Price, 1994), than the different environments driving rapid development to avoid predation of larval stages.

What is of particular interest in these results, is the differences between the three *Spatulonthus* species, and whether or not those differences can be explained in terms of adaptation to the biotic or abiotic environment. The general picture to emerge is one of slight, but significant, differences in developmental rate, developmental threshold, and upper lethal temperature. *P. incognitus* and *P. labdanus* appear as cool adapted species, with higher rates of development at lower temperatures, lower developmental thresholds and reduced upper lethal temperatures. In comparison, *P. sanamus* has a higher rate of development at higher temperatures, a higher developmental threshold and a higher upper lethal limit. These results are in reasonable agreement with predictions generated from the local and continental distributions of these species. This agreement suggests thermal adaptation of some nature. To deduce if these adaptations are sufficient to constitute different thermal niches one then needs to look at what effect differential developmental rates will have on the period of time spent by the larva in the pat, when it is vulnerable to predation, habitat destruction and food restrictions. Table 3 shows that *P. sanamus* at 15 °C would be exposed to these threats for up to four days longer than the other two species. But from 20 °C upwards there is virtually no difference between the three species in the time spent in the dung. The egg and pupal stages follow a similar pattern, so that overall *P. incognitus* and *P. labdanus* would appear to be more cold adapted than *P. sanamus*, but only at a real advantage in markedly cooler habitats. In hotter areas *P. sanamus* would develop most rapidly. These physiological traits may go some way to explaining the occurrence of the former species at Innisfree and Cluny farms. However, these differences in developmental rate could easily be ameliorated by diurnal migration of the larval beetles in the dung in response to temperature gradients.

Dung pats provide temperature heterogeneity in space and time. The difference between dung crust and core temperature can be considerable (Landin, 1967; Lipkow, 1982; March and Bay, 1983), as can the diurnal and seasonal fluctuation. Temperature differences between sun and shade will also be large. Adult beetles

could use thermal cues to maintain themselves at different optimal temperatures in a thermally patchy environment. If optimisation is a reality, the benefits to beetle larvae to do the same are clear, an animal should feed in an area that maximises its fitness (Huey and Slatkin, 1976), which in this case would be accelerated growth in a rapidly changing temporary habitat. Consequently, *Philonthus* larvae should migrate up and down in a pat, as fly larvae have been shown to do (March and Bay, 1983), to maintain a specific optimal body temperature for growth. However, prey availability is probably of equal importance to temperature optimisation for larval beetles, therefore the same migration would then still be expected to occur; this possibility has not been examined in this study. The adult *Philonthus* examined would be expected to occupy somewhat different thermal habitats to each other, but results from Chapter 4 show that the three species overlap in time and space, in their utilisation of macro and microhabitat. However, Brown (1984) proposed that species with wide environmental tolerances are likely to achieve high local densities and be geographically widespread as *P. sanamus* is. Even though *P. sanamus* is the most abundant species at all three field sites, its numbers are lower in the cooler sites, while the other species exhibit the reverse trend (Chapter 4).

Thermal resource partitioning is dependent on habitat thermal heterogeneity and the scale across which these differences arise. If the thermal habitat is coarse-grained, species with different thermal requirements could partition the habitat on the basis of operative temperatures (Hertz, 1992). This may be happening to some extent in the gross distribution of these species, but overlap at the microhabitat level is complete. Overlap is predicted within such thermally fine-grained microsites as dung pats, because potential competitors are exposed to the same set of mobile prey items, predators, parasites and refuges (Hertz, 1992). Schultz and Hadley (1987) examined the distribution and physiology of two species of cicindelids. The adult tiger beetles showed different thermal physiologies, but overlapped in their habitat, without evidence of interspecific competition, and the larvae of both species were

found throughout the habitat. Schultz and Hadley (1987) concluded that the physiological tolerances of the beetles were conservative traits because they matched similar findings on other distant populations, from different habitats, of the same species. Coope (1979) asserts that the morphological stability shown by Cenozoic fossil Coleoptera was accompanied by physiological stability.

Lower developmental thresholds of the three species can be considered from the same view point in that they correlate with the distributions of each species. *P. sanamus* has a significantly higher threshold than the other two species, reflecting its wider distribution on the African continent. Surprisingly, *P. labdanus* has the lowest developmental threshold. *P. incognitus* and *P. labdanus* therefore will be able to develop in cooler areas or at cooler times of the year. As these species are not found in shaded habitats (Davis *et al.*, 1988; Davis, 1996a), it is reasonable to suppose that they are better adapted to life at higher altitudes or latitudes than *P. sanamus*. If there is a trade-off in temperature adaptation, which has not always been found to be the case (Mongold *et al.*, 1996), then *P. sanamus* may gain by being able to tolerate higher temperatures as an adult.

The developmental data are well supported by the lethal temperature study, as adult *P. sanamus* can tolerate temperatures up to 2.3 °C hotter than *P. labdanus*, and 1.7 °C hotter than *P. incognitus*. The upper lethal limit of each species correlates with their different lower developmental thresholds, and it is notable that again *P. labdanus* has the lowest value for this parameter of the three species. The differences between species are not large, but they are significant and conceivably could confer an advantage on an animal that may forage below the crust of dung pat, where the temperature can surpass 45 °C. However, the adult beetles have been found to overlap extensively in their choice of habitat, so that segregation based on lethal dung temperatures is unlikely to occur, or be the evolutionary force behind these differences, because the pat offers refuges from extremes of heat. Where these physiological differences may play a role is in the tolerance of high temperatures in

the upper strata of the pat where fly larvae and other prey migrate during the course of the day (Valiela, 1974; March and Bay, 1983). The horn fly *Haematobia irritans* (L.) has an upper lethal temperature of 37 °C (Palmer *et al.*, 1981), which is substantially lower than that of these potential predators. Lower lethal temperatures of the study species would be useful to compare for correspondence with the upper lethal limits, because all three species are found throughout the year, and at sites where frost occurs in winter.

Physiological differences between species have been used as evidence of character displacement in desert foraging ants (Marsh, 1985; Christian and Morten, 1992), where temporal separation is considered to play an important role in species co-existence (Hölldobler and Wilson, 1990; Cerda *et al.*, 1997). This temporal separation has not been noted in the behaviour of these *Philonthus* species as they are found in the same strata of pats at the time of sampling (Chapter 4). Several questions now arise. Can these data be used to describe the thermal niche of each species? To some extent, they can because upper extremes of tolerance and lower thresholds of development largely encompass the important climatic variables that the species will be able to cope with. Secondly, the thermal range experimentally determined for each species correlates fairly well with the distributions of each. Given that each species has a different thermal niche, can this adaptation be attributed to character displacement? This conclusion appears to be unlikely as immature beetles will spend similar amounts of time in the pat at average summertime temperatures and the overriding pressure will be to develop as rapidly as possible before the pat is either destroyed or dries out, as has been found with *Drosophila* larvae developing in dropped fruit (Sevenster and van Alphen, 1996). Rates of development of the study species are of the same order of magnitude as those determined for other dung-breeding staphylinids (Hafez, 1939b; Prins, 1984; Hunter *et al.*, 1986). Each species has the potential to optimise speed of development by tracking favourable temperatures in the pat, but this will be balanced by presence of prey and avoidance of predators.

Teneral adults of each species will emerge at similar times and have to migrate to new pats to feed and reproduce. Sexual maturation is brief (about five days, Chapter 6). Therefore, all species are expected to be multivoltine and have their breeding synchronised by pat age rather than season. Each species has the potential to breed throughout the year, if the width of the temperature band that permits development is the same as that which permits reproduction, as is the case for many insects (Ratte, 1985; Atkinson, 1996).

Examining the developmental and temperature tolerance data presented, it can be concluded that there are physiological differences between the three *Philonthus* species with regard to their thermal biology. Using two independent parameters, one affecting immature development and the other affecting adult survival, the three species have .. shown to have the potential to occupy different thermal niches, matching their respective distributions. Although not widely reported, the link between physiology and distribution has been established in some species of insects (Schultz and Hadley, 1987), and even within populations of the same species of collembolan (Stam, 1997). Developmental rate and upper lethal temperature tolerance must be traits that have a genetic basis, and as such are subject to natural selection. There are two explanations as to why the study species should be adapted to different temperature regimes. The first is that what is being seen is the physiological adaptation to habitat segregation operating to keep the species apart and so avoid interspecific competition. However, Chapter 4 presents data to the contrary; these species co-occur in time and space. The alternative explanation is that the physiology of the species in question is part of its evolutionary baggage and not evidence of character displacement in the face of interspecific competition. Unfortunately it is difficult if not impossible to distinguish between the two explanations:

> "Historical and ecological information can be decoded from its species carriers, but rarely can the historical contributions of variations of geographical range be distinguished fro[illegible]ne ecological" (Martin-Pierra and Lobo, 1993).

Given the overlapping distributions of the three species of *Philonthus*, the thermal requirements of *P. incognitus*, *P. labdanus* and *P. santanus* look more like historical characteristics, which are the result of adaptation to climate during allopatric speciation, rather than character displacement due to competition. This supports the concept of stochastic community formation, maintained by primarily abiotic factors. The following chapters will look for evidence of character displacement in other aspects of the life- history of the three species and how these species react to competition when resources are limited.

CHAPTER SIX

COMPARISON OF LIFE-HISTORY TRAITS AND BREEDING BIOLOGY OF *P. incognitus*, *P. labdamus* AND *P. sanamus*

6.1 Introduction

In the previous chapter, it was shown that only very small differences exist between the thermal biology of *P. incognitus*, *P. labdamus* and *P. sanamus*. It was concluded that these differences are not sufficient to be used as evidence of niche separation, but rather match the large scale continental distribution of the beetles and could just as easily be attributed to different geographical origins of the species. Therefore, in addition to distribution and thermal physiology attributes, aspects of the life history traits of the three beetle species were examined for evidence of limiting similarity, or mechanisms that would keep the species ecologically separated. In addition, explanation was sought as to why *P. sanamus* was the most abundant species in all the material examined (Chapter 3).

Life history attributes refer to strategies employed by organisms to maximise efficiency or success and therefore life history traits feature directly in the reproduction and survival of organisms. Consequently, organisms have evolved many different ways of combining life history traits to improve survival and reproduction. The principal life history traits are: size at birth / egg size, growth pattern, age at maturity, size at maturity; number, size and sex ratio of offspring, age- and size-specific reproductive investment, age- and size-specific mortality schedules, and longevity (Stearns, 1992). These traits are bound together by numerous trade-offs, including current reproduction and survival, current reproduction and future reproduction, and the number, size and sex of offspring.

Schaffer (1974), proposed that a fluctuating environment that affects juvenile mortality more strongly than adult mortality will select for longer-lived adults, smaller clutch size, and reduced reproductive effort (i.e. that proportion of resources devoted to reproduction summed over the time interval in question). If environmental variability has its major effect on adult mortality, then large clutches, increased reproductive effort and short life span are favoured. These predictions require measurements of age-specific mortality patterns for the organisms in question, and can be considered in terms of the dung habitat, where mortality may be high for dung-dwelling larvae, but low for larvae protected in deeply buried brood balls.

A common thread of environmental pressures vs species density runs through most of the life history theories, that is most obviously represented in the r-K selection dichotomy. The familiarity and simplicity of the theory make it a useful tool for examining a species within its environment and, more importantly, allows comparisons of populations and species across phylogenies and habitats despite the apparent shortcomings of the theory. Viewing the r-K theory as a continuum rather than an all-or-nothing response makes it more useful for comparisons of species and predictions of what life history traits would be expected in a given habitat.

6.1.1 Life History traits of dung breeding insects

If one can characterise the habitat a particular animal is found in, one should be able to predict the life history traits of that animal, and vice versa. Looking at a dung pat, which is usually described as a patchy and ephemeral habitat (Doube, 1987; Hanski and Cambefort 1991e), one would predict that dung breeding animals would be r-selected, small in size, short-lived, and have short generation times and large clutch sizes. If the habitat is the driving force behind the evolution of life history strategies, then dung as a predictably unpredictable

habitat, would be expected to generate some sort of common pattern amongst the insects that inhabit it.

The reproductive strategies of most dung breeding flies would appear to fit the r-type pattern. Most produce relatively large numbers of eggs per clutch (20-100) which develop rapidly (Papp, 1970; 1975) and have several generations per season (Doube *et al.*, 1982; Fay, 1985). Larval mortality is very high, >90% in the horn fly (Thomas and Morgan, 1972). Larval densities can be very high (1000-2000/pat) for bushflies (Ridsdill-Smith, 1990), and about 2000/kg pat for horn flies (Palmer and Bay, 1982), levels which, amazingly are not high enough to cause an increase in larval mortality. However, these numbers do produce evidence of intraspecific competition, in that emergent adult headwidths are reduced, which in turn will reduce the number of eggs that those emerging females can lay (Doube and Moola, 1987).

Dung breeding flies generally show a boom and bust (r-selected) type of reproduction, in contrast to dung beetles, which exhibit a bewildering variety of strategies. An extreme K-type species, *Kheper nigroaeneus* (Scarabaeidae), produces only one brood per season, with very high immature survival, (69%) in the presence of the female (Edwards and Aschenborn, 1989), and is relatively long-lived (up to three years, Edwards, 1988). Alternatively, high fecundity, opportunistic breeders, such as *Digitonthophagus gazella* F. and *Euoniticellis intermedius* (Reiche), (both Scarabaeidae), may produce in excess of thirty broods in a single pat and survive as adults for only a few weeks (Doube, 1991).

The dung pat is in most respects a predictable environment, even though it is patchily distributed and short-lived. Undisturbed dung will dry out at a predictable rate (Byrne, 1988) and has a well-defined insect succession (Mohr, 1943). What is unpredictable is the amount of intra- and inter-specific competition that any beetle will face within a pat. Most beetles have an

aggregated distribution (Giller and Doube, 1994; Chapter 4). Exactly how strong competition for dung at the pat actually is, is still a subject of much conjecture (Giller and Doube, 1989, 1994). Anecdotal observations are usually biased by the impression a heaving mass of beetles makes on the observer, but optimal foraging behaviour has not been recorded in ball-rolling scarabs (Ybarrondo and Heinrich, 1996; Byrne, 1996), and beetles will often leave an unerowded dung pat, even abandoning fully formed balls. Locating fresh dung does not appear to be difficult, and most beetles are strong fliers, having been recorded flying over two kilometres from pat to pat (Byrne, unpublished data). Endocoprid beetles, which are most vulnerable to this potential competitive disturbance at dung pats, do not show an r-type response. For example, *Aphodius rufipes* (Scarabaeidae), a northern temperate species, lays eggs in batches of 6-8 scattered in the pat, and larval mortality ranges from 12-95% (Holter, 1979). Under extreme conditions which are usually climate induced, *Aphodius* larvae may leave the pat and burrow into the soil and feed on the brood masses of other scarab beetles (Lumaret and Iborra, 1996). Endocoprid *Onthicellus* species produce more eggs (7-20) in distinct brood balls, and avoid disturbance by breeding in older dung during the winter months (Davis 1977; 1989). However, for paracoprids and telecoprids, if the dung mass is deeply buried as a brood ball, then it may be considered to be a very predictable environment for immature development. This notion is supported by the extremely high survival rates recorded for *Kheper* species (Edwards, 1988; Edwards and Aschenborn, 1989). Nevertheless, the number of brood masses buried on each occasion, within the Scarabaeidae, may vary from 1 to 45 depending on the species (Doube, 1991). Clearly, even though they share a common, apparently homogenous microhabitat, dung beetles have widely differing reproductive strategies.

Investigations into scarab breeding strategies have centered around the evolution of nesting behaviour, rather than examining life history tactics (Halffter and Edmonds, 1982; Davis, 1989). Therefore the beetle size, and number of broods

produced per nesting occasion, are the most readily comparable data available. Among the scarabs the range of these parameters is impressive (Table 1). As expected, larger species produce fewer broods than smaller ones, but amongst the smaller beetles there is still a variety of tactics, and parental care may or may not be present. The telecoprids are restricted by their nesting behaviour to producing one ball per nesting occasion, although again there are exceptions to the rule. *Pachysoma striatum* (Scholtz, 1989) and *Scarabaeus galenus* (Ybarrondo and Heinrich, 1996) provision their nests in a telecoprid-like fashion, but return repeatedly to the dung mass to collect dung, which may be used to create more than one brood, representing an intermediate strategy to tunnelers and rollers. *K. platynotus* may sequester one enormous dung ball which is then subdivided into two or three smaller brood balls (Sato and Hiramatsu, 1993).

For dung beetles, size seems to be the most consistent predictor of reproductive strategy. Larger species are long-lived and have low fecundity. Parental care is exhibited by larger species in the genera *Kheper* and *Heliocopris* (Table 1), but there are not enough examples from other genera to generalise about this behaviour.

Looking at the other three main beetle families that inhabit dung, there is little or no information on their life histories. The Hydrophilidae are common, small beetles, coprophagous as adults and predatory as larvae, but virtually nothing is known about their life histories. As predators, some Histeridae have been introduced into Hawaii, Fiji and Australia as fly control agents, and some aspects of their life histories have been examined (Bornemissza, 1968). Females typically deposit one

Table 1. Life history characteristics of dung dwelling beetles.

Species	Size (mm)	TB	BN	BC	LF	GY	ID (days)	LO (days)	Source
Kheper nigroaeneus	28	R	1	Y	3+	1-2	130	1100?	Edwards (1988)
K. platynotus	28	R	1-4	Y	3-12	1?	?	1100?	Sato & Hiramatsu (1993)
K. aegyptorum	28	R	1-2	Y	3-6	1?	?	1100?	Sato & Imamori (1988)
Sisyphus sordidus	6	R	1	N	10-20	2	66	350	Paschalidis (1974)
S. seminulum	4	R	1	N	26	4	47	125	"
Neosisyphus mirabilis	10	R	1	N	47	3	77	144	"
N. fortuitis	10	R	1	N	55	2	73	154	"
N. sphilpes	9	R	1	N	44	4	52	104	"
N. rubrus	8	R	1	N	36	4	64	117	"
Hellocopris dilloni	50	T	2-7	N?	5+	2	180	180	Doube (1991)
H. japetus	50?	T	2-7	Y	2-7	1	240	365	Klemperer & Boulton (1976)
H. hamadryas	50?	T	6-9	y	6-20	1?	?	360?	"
Copris diversus	?	T	9-16	y			40		Tynedale-Biscoe (1984)
Onitis alexis	15	T	24	N	130		84		Edwards (1986)
O. caffer		T		N			168		
Bubas bison		T	16-20	N	60		88		Klemperer (1981)
B. bubalis		T					365-700		"
Hister chinensis	8-13	P	1-2	N	6-12	6	50	365+	Bornemissza (1968)
Platystethus arenarius	5	C	20-60	Y	?	3	29-35	?	Hi[illegible]
Philonthus sanamus	11	P	1-4	N	?	?	35	?	[illegible] 988)

Abbreviations as follows: TB, type of beetle (R, roller; T, tunneler; C, coprophage; P, predator). BN, number of broods per nesting occasion. BC, Brood care. LF, Lifetime fecundity. GY, generations per year. ID, immature development LO, longevity

or two eggs at the dung-soil interface, and larvae develop as free ranging predators within the pat. Dung breeding staphylinids are known to have several styles of reproduction, dependant on other life history characteristics of the genera. Predatory Staphylininae are notably similar to Histeridae, laying large eggs in small numbers at the base of the dung (Mank, 1923; Hafez, 1941; Hunter *et al.* 1986; Byrne, 1988). Parasitic Aleocharinae scatter tiny eggs in the substrate at the base of the pat, from where the larvae burrow into the substrate in search of their dipteran host pupae (Hertveldt *et al.*, 1984; Wright and Muller, 1989). Little is known about the coprophagous Oxytelinae, except that one species, *Platystethus arenarius* (Fourcroy), produces enormous batches of eggs which are protected by the female until all of them have hatched (Hinton, 1944).

6.1.2 Phylogenetic constraints

Overlaid on the effect of habitat will be the phylogenetic characters that will constrain the success of any organism (Price, 1994). Phylogenetic constraints set limits on the life history patterns that an organism can evolve. These are modified by "adaptive syndromes", that organisms evolve to maximise performance, which in turn influence the ecological interactions ("emergent properties") of such species (Price, 1994). Closely related species would be expected to have similar life history traits that will be modified by the overriding forces of the surrounding environment. If the biotic component of a habitat presents the strongest selection pressure, then a divergence in traits would be expected. Conversely, if the abiotic features of the habitat are the most powerful, then a convergence of adaptive syndromes is predicted.

The idea of the larval habitat as the primary driving force behind the evolution of life history tactics of dung dwelling Coleoptera does not appear to stand up to scrutiny. Paracoprids show a range of styles of reproduction as do telecoprids. Beetles breeding in the dung may be more at risk to a rapidly changing

environment, but still exhibit a variety of reproductive strategies. Size is one factor in which there is some consistency amongst the Scarabaeidae, where larger species tend to exhibit brood care towards a small number of offspring. But *Copris diversus* is an exception to this (Tyndale-Biscoe, 1984), and the small coprophagous staphylinid *Platystethus arenarius* (Hinton, 1944), does not fit comfortably anywhere into this trend.

It is evident that there is a vast array of life history traits that stretch from r to K tactics. What unifying theme could exist for these different tactics? Edwards (1988) proposes that for a K selected species like *K. nigroaeneus*, the habitat is predictable in that sufficient rain will fall each summer to allow breeding. Beetles that breed in the pat are not so dependent on rain, and may use adversity type strategies, avoiding competition by breeding in the winter months, as seen in some endocoprids. Other pat breeders, such as *Philonthus* species, may use bet-hedging tactics by leaving one or two offspring per pat to their own unpredictable fate. Adults of these species would be expected to be long-lived and large.

It is probably more instructive to look at differences in strategies within taxa that allow closely related species to exploit marginally different habitats. This has been shown even between different populations of the same species (Stam, 1997; Tatar *et al.*, 1997). *Heliocopris sp.* and *Kheper sp.* show precisely the sort of differences that might be expected between species. Unfortunately it is not always apparent what advantage such differences would confer under given circumstances.

In this chapter the life history traits of the three beetles were compared for specific differences that could possibly be attributed to the results of competitive character displacement, or taken as evidence of allopatric speciation. The influence of the dung micro habitat on the evolution of these traits is discussed.

6.2 Methods

The maturation, fecundity, egg viability, larval survival, longevity, and sex ratios of *P. incognitus, P. labdanus* and *P. sanamus* were measured in a variety of experiments.

6.2.1.1 Sexual Maturity

Age at first copulation was used as a measure of sexual maturity. Beetles were reared as described in Chapter 2. Emerging adults were sexed and isolated in 9 cm plastic petri dishes, where they were fed daily and kept as described in Chapter 2. Each day, individual beetles were tested for sexual maturity by assessing their readiness to mate. This was done by using similar methods to those described in Chapter 3. Virgin test subjects were paired with beetles of the same species and opposite sex, which were over 14 days old, and known to have mated. Each trial lasted for ten minutes, after which the beetles were returned to their original containers. Successful mounting, extrusion and intromission was taken as readiness to mate. The average number of days taken to mature was recorded for each species and compared using ANOVA.

6.2.1.2 Fecundity

Fecundity is usually defined as the number of offspring produced per unit time. Two time scales were used in these trials, therefore fecundity was measured in two ways. Firstly the numbers of offspring that reached adulthood, produced by a given female during her lifetime was counted, and secondly, the number of eggs laid by an individual female over a two week period was recorded.

For lifetime fecundity, approximately five pairs of adult beetles per species were set up in pots, as described in Chapter 2. Every week, the pairs were moved to fresh pots, and any beetles that had died were replaced. The vacated pot was fed and watered until the emergence of all the offspring, which were then sexed and

recorded as the progeny of a particular female. Mean numbers of offspring produced at a given age were used to estimate the age specific fecundity of each species. Because of the potential for both parental and sibling cannibalism in the lifetime fecundity design, daily oviposition rates of individual F1 females were measured. Eggs were collected daily by the method described in Chapter 2, from five pairs of each species, for a period of two weeks. Pairs of beetles were transferred to new pots with fresh dung on day 4 and day 8. The species rates of oviposition were compared using ANOVA.

6.2.1.3 Egg viability

Eggs were collected from females in laboratory cultures as described in Chapter 2, and kept separately on moist filter paper in 9 cm plastic petri dishes. Eggs were observed daily, and the hatching success for each species was scored and compared by means of a Chi-Squared test.

6.2.1.4 Larval survival

To determine if the laboratory rearing method had any differential effect on the survival of immatures of each species, 20 first instar larvae of each species were reared to adult using the pot method described in Chapter 2. Adult emergence was recorded for each species and compared using a Chi-Squared test.

6.2.1.5 Longevity

Pairs of F1 adult beetles were kept in pots as described in Chapter 2. The beetles were fed *ad libitum* and moved to fresh pots weekly. Beetles that died were replaced. Longevity was recorded for each species, and then compared using ANOVA.

6.2.1.6 Sex Ratios

Sex ratios for field populations were taken from monthly collection data (Chapter 4). The sex of beetles emerging in laboratory cultures was used to determine

ratios in the laboratory population. Results were transformed to percentages, then numbers of males and females for each species were compared using a Wilcoxon signed ranks test.

6.3 Results

6.3.1.1 Sexual maturity

The age at first copulation for the three species is shown in Fig. 1. Female *P. labdanus* matured significantly younger than *P. sanamus* females ($F = 4.708$; $df = 2,60$; $P = 0.013$), and there is no difference between other combinations of females (Tukey HSD). There is no significant difference in the maturation age of males of all three species. Both female *P. incognitus* and *P. labdanus* mature earlier than their respective males ($F = 22.31$; $df = 1,37$; $P < 0.001$, and $F = 35.82$; $df = 1,24$; $P = 0.001$ respectively). There is no significant difference between male and female *P. sanamus* maturation times ($F = 0.54$; $df = 1\ 39$; $P = 0.475$).

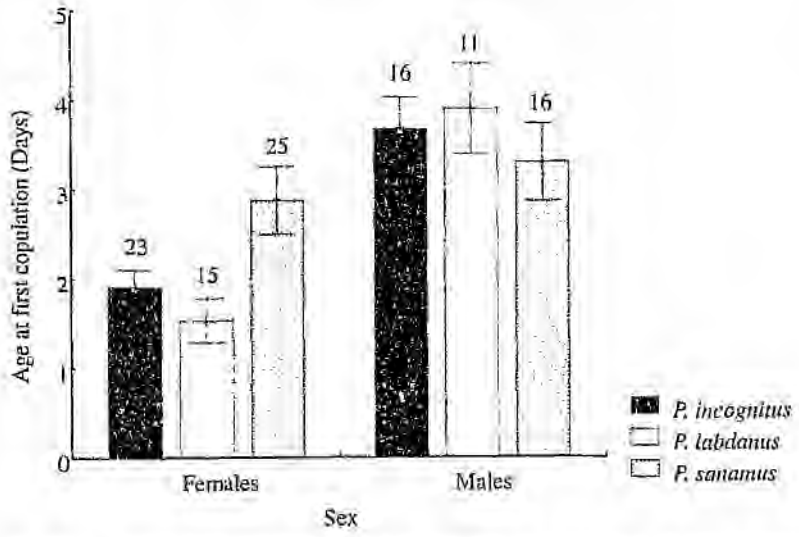


Figure 1. Age at first copulation for three species of *Philonthus*. Totals above each bar denote the number of each species tested. (Error bars = 1SE).

6.3.1.2 Fecundity

No significant differences were found among the three species in total numbers of offspring produced by each female ($F = 3.244$; $df = 2,14$; $P = 0.070$; Fig. 2). However, female *P. sanamus* produced fewest adult offspring, and significantly fewer eggs per female per day, ($F = 16.15$; $df = 2, 192$; $P < 0.001$; Fig. 3).

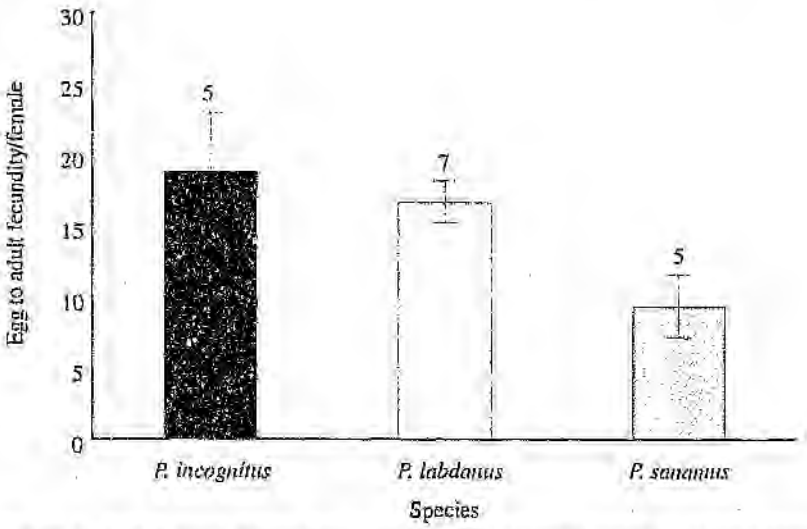


Figure 2. Egg to adult female fecundity of three *Philonthus* species. Totals above each bar denote the number of females observed. (Error bars = ISE).

All species laid large eggs, usually singly, every day. However, daily totals fluctuated with the age of the dung (Fig. 4). The two weeks were divided into three periods, delimited as days 1- 4, 5 - 8 and 9 - 12. A linear regression was performed of individual daily egg production against these periods. No significant relationship between dung age and oviposition rate was detected for any species. *P. incognitus* ($F = 0.003$; $df = 1, 63$; $P = 0.958$, $r^2 = 0.000$), *P. labdanus* ($F = 0.512$, $df = 1, 63$; $P = 0.477$, $r^2 = 0.008$), *P. sanamus* ($F = 0.046$; $df = 1, 63$; $P = 0.830$, $r^2 = 0.001$).

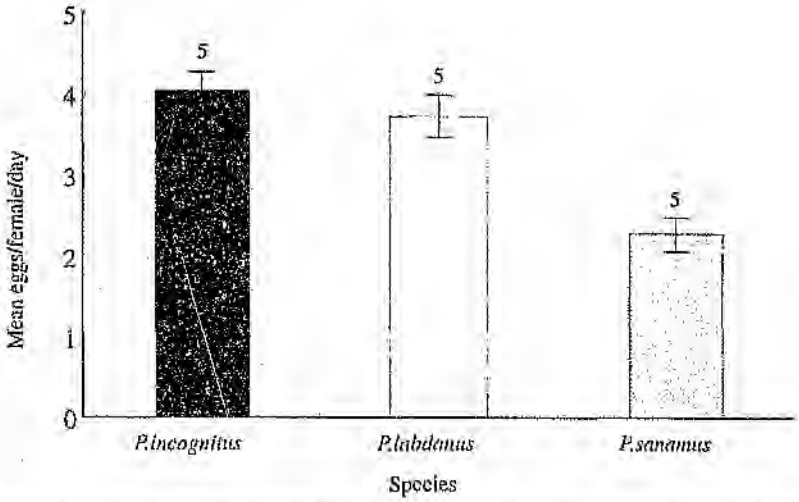


Figure 3. Mean daily oviposition rates of female *Philonthus* over a two week period. Totals above each bar denote the numbers of females observed. (Error bars = 1SE).

Egg to adult fecundity data were used to generate age-specific reproduction curves for each species. The curves for each species are roughly the same shape in that females start laying at a similar age, produce offspring at a fairly constant rate throughout their lifespan and continue to breed until shortly before death (Fig. 5).

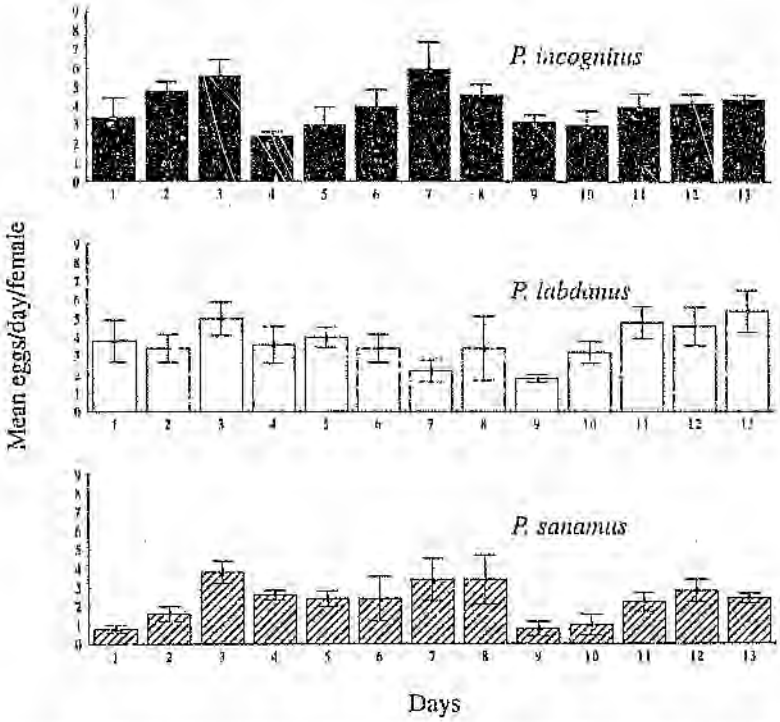


Figure 4. Fluctuation in daily oviposition of three *Phllonthus* species. n = five females per species. Dung was changed on day four and day eight. (Error bars = ±SE).

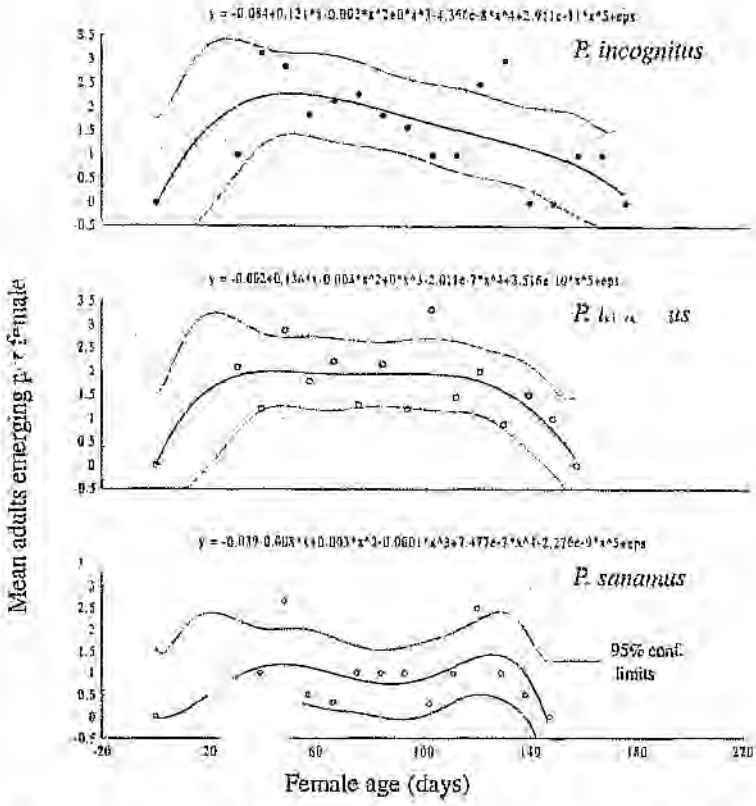


Figure 5. Age specific fecundity (egg to adult) of three female *Philonthus* species.

6.3.1.3 Egg viability and immature survival

Levels of egg viability were high for all species (Table 2) and not significantly different between species (Chi-square = 0.0287; df = 2; P = 0.985). Larval survival from L1 to adult was relatively high (Table 2), with no difference between the species (Chi-Square = 0.2692; df = 2; P = 0.874).

Table 2. Fertility of eggs, and immature survival of three *Philonthus* species.

Species	Fer..lity		Survival L1-Adult	
	n	% Hatch	n	%Survival
P. incognitus	92	97	20	80
P. labdanus	92	99	20	95
P. sanamus	92	97	20	85

6.3.1.4 Longevity

Figure 6 shows the average female lifespan for each species. *P. incognitus* females are significantly longer-lived than females of the other species ($F = 4.515$; $df = 2, 95$; $P = 0.013$).

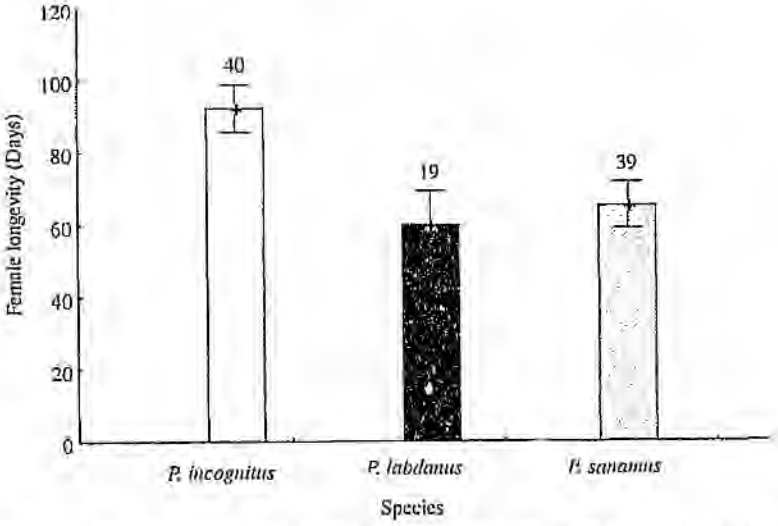


Figure 6. Female longevity of three *Philonthus* species. Totals above each bar denote the numbers of females observed. (Error bars = 1SE)

Using these data, and those from fertility and immature survival, survivorship curves were drawn up for each species (Fig. 7). The shapes of the curves were compared using ANCOVA (Rudestat, Lighton, 1994), and found to be similar

among the species (F = 0.924; df = 2, 92; P = 0.400). No species showed marked mortality at any specific life stage.

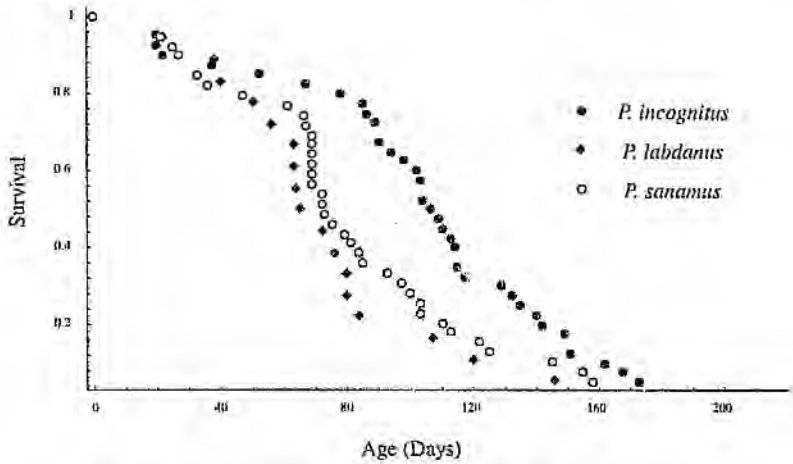


Figure 7. Survivorship curves for three species of *Phillanthus*.

6.3.1.5 Sex ratios

Skewed sex ratios were noted in field populations of *P. incognitus* and laboratory populations of *P. sanamus*, but no significant deviations from one were found in any of the species (Table 3).

Table 3. Sex ratios (male:female) of field and laboratory populations of three species of *Philonthus*. Field n = months of pat collections. Lab. n = rearing trials. P value from Wilcoxon signed ranks tests.

Species	Males	Females	Sex ratio	n	P
Field					
P. incognitus	59	34	1:0.58	8	0.270
P. labdanus	50	54	1:1.08	8	0.916
P. sanamus	237	231	1:0.97	12	0.593
Laboratory					
P. incognitus	76	74	1:0.97	6	0.343
P. labdanus	76	71	1:0.93	6	1.000
P. sanamus	85	63	1:0.74	7	0.109

6.4 Discussion

Of the life history traits examined, few statistically significant differences were found between *P. incognitus*, *P. labdanus* and *P. sanamus*. These findings can be summarised as follows.

P. labdanus females mature earlier than *P. incognitus*, and significantly earlier than *P. sanamus* females. Age at first reproduction is considered to be more important than clutch size for colonising ability. Therefore selection should be stronger on developmental time, than on fecundity. As animals that have to continually seek out and colonise new habitat patches, *P. labdanus* would be expected to be a superior coloniser to *P. sanamus*. However, all species will reach sexual maturity within three days of emergence. No differences were found between the maturation period for the males of the three species.

P. sanamus had the lowest fecundity of the three species, measured as daily oviposition rate and total lifetime fecundity. The more rapid sexual maturity and higher oviposition rates recorded for *P. labdanus* and *P. incognitus* could be a reflection of the thermal physiology of the two species, as these trials were conducted towards the upper end of their preferred temperature range (Chapter 5). However, all these trials were run at 25 °C, at which *P. sanamus* is expected to perform at least as well as the other species. In addition, all trials were run on F1 laboratory populations reared from adults caught at Cluny farm. One cannot assume that the expression of an organism's genome is constant across environments, and gene-by-environment interactions are expected. Mertz (1975), found changes in fecundity and developmental rates of *Tribolium* in 11 - 12 generations, as an adaptation to novel conditions. Therefore, one would anticipate some form of adaptation of all three species to the same climatic conditions at the Cluny site.

The fecundity of the three species is relatively low, and all species produce large eggs, scattered singly or as small clutches in the dung. In cases where juvenile survivorship is low, long adult life and iteroparity and low fecundity (juvenile investment) are predicted (Toda and Kimura, 1997), and a bet-hedging tactic is expected. Because *Philonthus* larvae cannot escape their natal habitat until metamorphosis, the larval stage of the beetle's life-cycle will be the most vulnerable to predation and habitat destruction, and survival will be low or unpredictable. Other life-history data support the notion that *Philonthus* might be bet-hedging. Eggs are laid throughout the lifespan of the female (Fig. 5), at a similar rate by all species, and adults of each species spend no more than four or five days at a given dung pat (Chapter 4). Therefore the dung pat will support the development of only one generation of beetles, and this is presumably the most unpredictable stage in the beetle's lifecycle, because the pat could be totally removed by scarabs, or devoid of suitable prey species, making juvenile mortality

high. Newly emerged adults will have to leave that pat and fly to a new one where they will mature rapidly and lay eggs in that habitat or the next one encountered.

Egg viability and larval survival of individuals reared separately were high (Table 2), but lifetime fecundity of all species was low in the laboratory. This may be an indication of the vulnerability of the egg and larval stages to cannibalism. Although this was only rarely observed in these laboratory cultures, *P. decorus* adults have been found to eat their own eggs (Heessen, 1980), and the larvae are cannibalistic, even at very low densities (Heesen and Brunsting, 1981).

Adult beetles of all species were found to be reasonably long-lived, *P. incognitus* longevity being significantly greater than that of the other two species. Survivorship curves of all species were a similar shape showing a fairly constant rate of mortality through the lifespan.

Comparing the life history traits of dung breeding *Philonthus* to those of other dung dwellers, generation time and adult size appear as the best predictors of reproductive strategy (Table 1). However, dung breeding flies are of a similar size to the species of *Philonthus* observed in these trials. Flies are generally iteroparous, but produce medium to large clutches (12 - 200) of small eggs. The adults are fairly short-lived and the larvae develop rapidly. Although most insect species delay development beyond what is physiologically possible, some calliphorids and muscids (Palmer *et al.*, 1981), can complete their development in 50 hours under optimal conditions. Overall, dung-breeding Diptera can be considered to be more r-selected in their life history traits than *Philonthus* species. Given that their developing larvae are faced with the same uncertainty as immature *Philonthus*, what then explains this marked divergence in life history strategy between the two insect families living in the same microhabitat?

The mortality schedules of the two orders may be markedly different even though the larvae share the same habitat. *Philonthus* are assumed to be tied to the dung habitat throughout their whole life, apart from migratory flights between pats. Adult flies on the other hand may live away from dung, feeding on proteinacious liquids. If adult mortality in this environment exceeds larval mortality in the dung pat, then increased reproductive effort and short life span are favoured (Stearns, 1976). This idea is attractive in that it supports Stearns' (1992) suggestion to discard r and K-selection, and couch explanations of life histories in terms of mortality schedules rather than habitats for greater simplicity and generality. Nevertheless, he does not exclude the K (density dependent) component of the r and K theory, and, given the body of evidence relating habitat to life history (Southwood, 1977; 1988; Toda and Kimura, 1997), he suggests that habitat can be linked to a life history theory through mortality regimes (Habitat → Mortality regime → Life history). Nevertheless, larval mortality of fly larvae is known to be very high in dung pats (Thomas and Morgan 1972; Thomas *et al.*, 1983), and likely to surpass that in the non-dung habitat.

If examination of the hypothesis of mortality schedules driving life history traits is extended to other dung breeding species, some support for mortality schedules as a major influence in life history traits is seen. Most telecoprid Scarabaeinae are phylogenetically constrained to produce only one brood ball per nesting occasion. Small telecoprids in the 5 - 10 mm range (e.g. *Sisyphus*), are relatively long-lived and moderately fecund. Some species such as *S. spinipes* Thunberg do not bury brood balls, but suspend them in vegetation where the developing larvae will be more vulnerable to biotic and abiotic threats than those of larger telecoprids, buried deep beneath the soil. Because of their ball-rolling behaviour, which restricts them to creating only one brood ball for each new dung pat they colonise, *S. spinipes* has to adopt a bet-hedging strategy, producing fewer offspring over an extended lifespan. In contrast, *Euonitiocellus intermedius* and *Digitonthophagus gazella* are also small (10 - 15 mm) scarabs, but their paracoprid breeding strategy

allows them to produce up to thirty broods on each breeding occasion. Both species develop rapidly, have a large reproductive output, and are short lived (Table 4).

Table 4. Life history parameters of four species of dung beetles. *Euoniticellus intermedius* and *Digitonthophagus gazella* are small paracoprids. *Sisyphus seminulum* is a small telecoprid, and *Philonthus incognitus* is a medium sized staphylinid.

Species	*E. interme* *s* *	*D. gazella* *	*S.seminulum* †	*P. incognitus*
Development (days)	28	41	53	31 (20 °C)
Lifetime fecundity	120	90	43	19
Longevity (days)	45	60	104	106

Data from * Rougon and Rougon, (1991), † Paschalidis (1974).

Other staphylinids such as *Aleochara* produce large numbers of tiny eggs (Hertveldt *et al.*, 1984; Wright and Muller, 1989). The hatching larvae burrow into the soil in search of fly pupae, in which they continue their development (Greene, 1997). While larval mortality may be low in this protected environment, it is likely that the adults are subject to precisely the same mortality schedules as *Philonthus* adults. Looking at other *Philonthus* species, the oviposition behaviour seems to be conserved across the group. Small numbers of large eggs are typically scattered in the dung (Hunter *et al.*, 1989), or soil (Eghtedar, 1970; Heessen, 1980). This is possibly a phylogenetic constraint of the group (Price, 1994).

However, Price (1989) provides an alternative explanation for this convergence of behaviours in different habitats, which he describes as a preference - performance linkage in female behaviour, or "mother knows best". Females select microhabitat oviposition sites where their larvae will survive and develop best, providing a strong feedback selection pressure on behaviour. This effect has been shown in sawflies from a wide variety of sites (Price *et al.*, 1987; Price and Ohgushi, 1995),

and contrasts with oviposition behaviour where the female is unable to evaluate the quality of the larval resource (Price, 1990). Although no firm evidence of this linkage was found in the current trials, the fluctuation of oviposition rates seen in the laboratory (Fig. 4), despite unvarying food quantity and quality because of daily feeding, suggest some type of adaptive behaviour by the females. Attempts were made to assess oviposition preferences of female *Philonthus* in the field by washing eggs from dung pats of different ages, but unfortunately the eggs proved too difficult to retrieve from the pat samples.

Females of the experimental species mature rapidly. This strategy can be seen as an adaptive syndrome (Price, 1994), as a response to the newly emerged adult beetles having to search for a fresh dung pat which in turn will only support one generation of offspring. What is notable is that this abiotic pressure has caused convergence between the three study species as they all mature very rapidly. The habitat appears to be pushing them together, rather than the other species forcing them apart.

The question arises then - why are the differences between the species so small? The two potential reasons are encapsulated in the title of Hutchinson's (1965) book, "The Ecological Theatre and the Evolutionary Play" where he develops the theme that ecology sets the scene for evolutionary processes. Price (1994) argues that this view is appropriate only on a microevolutionary scale, and the reverse notion, that the phylogenetic history of a species provides strong influences on its current ecology, is more appropriate to viewing large scale patterns in nature.

Of the two, Hutchinson's view would appear to be more appropriate in this case. The life expectancy of the dung pat is a strong synchronising force on the development of the experimental species and will select for rapid development and maturity. The habitat then would appear to be the template upon which the *Philonthus* life history patterns have evolved (Southwood, 1977).

If the rapidly changing dung habitat has driven life history evolution in these species, why then are there any dissimilarities in life history traits between the beetles studied? If the constraints of their habitat have caused convergence of the characteristics examined why hasn't there been a complete overlap of these traits? It seems likely that these slight differences are phylogenetic constraints, which adaptation to local conditions has still not eliminated. Although less easily explained than the thermal physiology of the species, these differences do not appear to be mechanisms of coexistence.

P. incognitus and *P. labdanus* are the quickest developers, most fecund, and longest lived, yet *P. sanamus* is the most abundant of the three species. Two possible explanations come to mind. Firstly, that cattle dung is not the preferred habitat of *P. labdanus* and *P. incognitus*. Davis (unpublished data) has collected *P. labdanus* using rotten grass bait, and one of the few specimens in the BMNH collection was taken from rotten grass at "Zoo Lake Park" (Appendix) Similarly, several of the *P. incognitus* specimens at the BMNH bear the labels "collected from the inflorescence of *Lobelia rynchopetalum* or soil nearby". Trapping with the "wrong" bait may lead to the erroneous assumption that particular species are rare (Davis and Sutton, 1997). Nevertheless, if their occurrence in dung is purely coincidental, then why do *P. incognitus* and *P. labdanus* do so well in it, compared to a species that has only ever been recorded from dung? The second, more persuasive, explanation is that *P. sanamus* is a better competitor than the other two species, and that direct interference competition does have a hand in shaping this small section of the dung community. This idea is explored in the next chapter.

CHAPTER SEVEN

EVIDENCE OF COMPETITION BETWEEN *P. incognitus*, *P. labdanus* AND *P. sanamus*

7.1 Introduction

This chapter explores the evidence for competition between the three species of *Spatulonthus* under study. The absence of any obvious mechanisms of coexistence in the results gathered thus far can be interpreted in two ways. Firstly, that the competitors have evolved away from each other, Connell's (1980) "ghost of competition past"; or secondly, that resources are not usually limiting and the species concerned are never in a situation where competition is likely to occur. Therefore any differences that exist between the species can be explained as historical features of the ancestral population. This chapter explores current competitive effects between the species and looks for evidence of past competition in the individual body size of different populations of the species.

7.1.1 Size

Size is a fundamental character of any organism, as much as any other life history trait, and has far-ranging consequences on all aspects of animal ecology (Peters, 1983; Schmidt-Nielsen, 1984). Morphological adaptations are generally agreed to be evolutionary responses to ecological conditions (James and Boecklen, 1984). It makes sense to expect any organism to be somehow matched in size to its habitat and resources, including prey. The problem arises in trying to ascribe the presence of a competitor to the role of an ecological condition. The first assumption therefore, is that there is some correspondence between the character being measured and the position along the Resource Utilisation Frequency (RUF), an

axis that describes, for example prey size. However, Abrams (1990), contradicts this point of view. The second assumption is that variation in the character is at least partially heritable (Keddy 1989). Morphological characters tend to have fairly high heritability values (Arthur, 1987) and phenotypic size effects in insects are well documented (e.g. Krasnov *et al.*, 1996; Doube and Moola 1987; Ridsdill-Smith and Hayles, 1989). But, size in scarab dung beetles has been found to have a low heritability, being heavily influenced by environmental factors particularly food quality and availability (Cook, 1993; Emlen 1994; Hunt and Simmons, 1997).

Nevertheless, the expectation is that size is an adaptive trait, and if this is so then sizes should differ between coexisting species, as a result of some form of character displacement, limiting similarity. This is essentially an historical method of looking at past exploitative competition and can be used on both a local and regional scale.

7.1.2 Species as adaptive devices

Adaptation is an important feature of biological entities, occurring as a result of natural selection. Adaptation is commonly caused by directional selection which is easy to produce in the laboratory, but less so in the field. Nevertheless, industrial melanism and insecticide resistance are just two of the best known examples. Therefore, we must accept that animals can adapt in response to a selective pressure, but the important question is to what extent does this affect competitive ability? Are adaptive features products of competition or the environment? Or, turning the question around, is competition a sufficiently strong directional force to cause species-wide adaptation? Schluter (1984) concludes emphatically yes, and later (1994), provides convincing supporting evidence. But the Achilles' heel still remains a logical way to extend adaptations throughout a species' range without invoking group selection (Walter *et al.*, 1984). Adaptation

is seen only as fine tuning a species to its habitat, which may include potential competitors, but not as a mechanism for creating communities. The implication of a fine-tuned, optimal organism, akin to some paragon of engineering is a fallacy. "Imperfection abounds in nature because the solutions to functional demands bear the stamp of history and ancestry, and are often clumsy and ad hoc" (Vermeij, 1994).

7.1.3 Character displacement

Differences in some characters between species in sympatry are often seen as mechanisms of avoiding competition. These differences which cause resource partitioning, are due to genetic change in a species called character displacement (Brown and Wilson, 1956). Grant (1972) has restricted the term to morphological changes, which is reasonable as most studies of character displacement have been morphologically based, and size and shape usually have high heritability values (Arthur, 1982). The expected outcome of competition in sympatry is that the larger species will get larger and the small species get smaller. The literature is thick with examples of character displacement, particularly in birds (Schoener, 1984 is a notable example), but insects (Chown, 1992), and dung beetles (Hybosoridae, Hanski and Cambefort 1991), are also covered. These data are satisfying as they fit very neatly with the theories of competitive exclusion and limiting similarity. But as a simplistic explanation, most of these studies are open to alternative explanations, as some of the authors will concede, the most obvious of which is clinal gradients (Arthur, 1982). Mimicry and hybridisation are other alternative hypotheses (Arthur, 1987). Very few studies have been able to conclusively demonstrate character displacement resulting from competition. It may happen in some circumstances, and competition may reduce genetic variabil. y of character under examination (Arthur, 1982). Nevertheless, character displacement remains one of the few ways to measure the ghost of competition past (Connell, 1980), and some convincing studies have been done (Schoener,

1984; Schluter, 1994). Central to the whole problem is ensuring that there is a link between the character measured and the niche axis, and that the character is heritable.

7.1.4 Convergence and Divergence

Convergence, divergence or extinction are the expected outcomes of competition. Convergence is less common, but Abrams (1990), persuasively argues for its potential existence. Such evidence as there is comes from sympatric convergence of bird song, although this can be explained away in many cases by mimicry or hybridisation (Arthur, 1987). Convergence is more easily explained as evidence of constraints of the environment. Divergence in character is seen more often (Schluter, 1994), but to be considered adaptive, the change must be genetic, causing a shift in the "potential niche". This is difficult to prove and requires well designed explant experiments (Keddy, 1989).

The notion that size could be limited or acted upon by competitors was formalised by Hutchinson (1959). In asking the question, "why are there so many animals?" he concluded that natural selection causes limits to similarity, constraining animals to certain size ratios relative to their neighbours. The magic ratio of 1 to 1.3 was "tentatively" proposed as being the ideal difference between competing species. The fact that this was the ratio discovered by Dyar, between successive headwidths of Lepidopteran larvae (Richards, 1949), led to the comfortable feeling that it was a law of nature. In addition, it was a neat easily measured and easily understood addition to competition and niche theory that led to a plethora of papers, some supporting, others refuting the Dyar-Hutchinson rule. Subsequently, the idea was incorporated into the competitive exclusion principle, which states that identical competitors cannot coexist, or turning it around, that resource partitioning is the sole mechanism by which "species undergoing exploitative competition reach a state of stable coexistence" (Arthur, 1987). It is assumed that

niche differentiation is the principle mechanism organising communities. If this is correct, then it is difficult to explain how similar species can coexist. Species with similar niches would be expected to experience intense competition between them, forcing one species to extinction. This idea has been called the competitive exclusion principle (Hardin, 1960). The theory is well supported by laboratory experiments (Park, 1948; 1954; 1962), leading to the conclusion that "ecological differentiation is necessary for coexistence" (Hardin, 1960). The main drawback of the principle is how similar is similar? There is no real measure of this other than coexistence, in which case the conclusion is that they are sufficiently different; if they do not coexist then one concludes that they are too similar. The argument is circular, being able to explain either outcome. Size is an obvious measure of similarity, but is always open to the possible criticism that it is an inappropriate measure of similarity. Size will affect many aspects of biology, not least the food which an animal can select. Therefore the sizes of sympatric species are expected to be spaced out along a resource axis related to food size. There is some support for this theory from sizes of smaller *Aphodius* (Hanski, 1991), *Phanaeus* (Kohlman, 1991), and some telecoprids (Cambefort, 1991). But whether this apparent regularity constitutes proof of past competition has been the subject of much debate (e.g. Strong *et al.*, 1984). The argument has centred around the application of "null models" used to statistically test if the size distribution of coexisting species differs from a random distribution (Simberloff and Boecklen, 1981). Criticism has been levelled from all quarters and Roughgarden (1983), has described null models as no more than rearranged species lists. The main problems with this method are that the data set is often being tested against itself, so it is not surprising that differences are hard to find. Evolutionary disagreements stem from the fact that the evolutionary history of a species alone will restrict its potential distribution along a resource gradient (Walter *et al.*, 1988). Finally, the expectation that all points along a resource gradient will be equally advantageous is unlikely (Abrams 1990), and difficult to demonstrate (Walter *et al.*, 1988). Large numbers of species are also required to

construct a useful null model (Schoener, 1984). The fact that well spaced size ratios are also found in kitchen utensils (Horn and May, 1977) suggests that we may be trying too hard to make something fundamental out of these patterns in nature. If there is a limit then it may be reasonable to suspect that this is variable (Abrams, 1983).

7.1.5 Size and Dung Beetles

Size variation covers four orders of magnitude in dung beetles from tiny 1 mg *Panelus spp.* to 10g *Heliocopris* species (Hanski and Cambefort, 1991b) Size will affect the range of food that can be used and larger beetles will be restricted to the droppings of larger animals. Chown *et al.*, (1995) propose that the now limited distribution of the large telecoprid *Circellium bacchus* is due in part to its dependency on the dung of rhinoceros and elephants. This effect will be reversed with predatory beetles, where larger beetles should be able to use a greater size range of prey species, and presumably have a competitive advantage (Wilson, 1975). Coprophagous beetles have other profound morphological differences between the different guilds related to the way in which they sequester dung. The different shapes and sizes of telecoprids and paracoprids may represent trade-offs between efficient tunnelling and efficient running which may contribute to niche differentiation and reduced competition for space under the pat (Duncan and Byrne, 1997).

General reviews of competition (Schoener, 1983) reveal most competition between granivores, nectivores, carnivores and scavengers, and more often between larger rather than smaller individuals. This is reflected in the distribution of dung beetles. Kohlman (1991) found small beetles to be more aggregated than larger species, which tended towards a density dependant distribution, as did specialist species when compared with generalists. Abundance may also be influenced. If two similar sized species (size ratio 1.05 - 1.25), occurred in the

same community, then one tended to be very rare. Between less similar species (size ratios 1.37 - 1.46), the asymmetry in abundance was "less striking" (Kohlman, 1991). With regard to lineage effects, size not tribe is found to influence aggregation more strongly (Hanski and Cambefort, 1991b). In pat dwelling species, Hanski (1980a) found body sizes in species of *Sphaeridium* to be better spaced out than those of *Aphodius* species, which he concluded were seasonally separated. *Sphaeridium* adults are coprophagous, but the larvae are pat dwelling predators. Hanski (1980a) considered that the smallest of three coexisting species of *Sphaeridium* was "doing the worst" not the middle-sized species, contrary to the predictions of May and MacArthur (1972).

7.1.6 Competition

Intraspecific or interspecific interactions describe types of competing entities. Intraspecific competition is often assumed to be strong and logically should be the most consistent selective pressure. Competition between genotypes can be investigated in this regard. Interference competition is predicted to be intraspecific, but again is not always found (e.g. Hattingh and Samways, 1990). Interspecific competition and its role in community formation is a subject of controversy (Strong *et al.*, 1984) and therefore of interest. Despite limited evidence (Arthur, 1987), it is assumed to be important and may be symmetric or asymmetric. Asymmetric competition results in one species being competitively dominant. This type of dominance, achieved by either interference or exploitative competition must be separated from simple greater abundance. The former species has traits for suppressing its neighbours, while the latter may achieve its dominance through traits for tolerating the environment (Keddy, 1989).

Along with predation and mutualism, competition, despite its elusiveness, is seen as one of the fundamental forces in communities. It can be defined as the negative effects that one organism has upon another by consuming or controlling access to

a resource that is limited in availability. Measuring this effect in heterotrophs is complicated by the fact that the resources come in packages (plants or animals) and in many cases these packages are substitutable (Wiens, 1984; Vincent *et al.*, 1996), particularly for predators.

The competitive interaction may take several forms, as may the types of entities interacting. Competition is usually either exploitative or interference. Heinrich and Bartholomew (1979) recorded both types of competition in *Kheper laevistriatus*, a nocturnal telecoprid. The first beetles to arrive at droppings were more likely to be able to remove dung more rapidly and were therefore more successful at exploitation competition. In addition, fighting took place over dung balls (interference competition) and again the larger, warmer beetles were the most successful. So competitive ability in this species could be predicted by two straightforward variables - size and body temperature. Much of the other evidence for competition in dung beetles is anecdotal (Matthews, 1963; Tribe, 1976). Giller and Doube (1989) are a notable exception to this.

7.1.2 Aims

From the results of field collections (Chapter 4) *Philonthus sanamus* can clearly be described as the dominant species in the troika. *P. sanamus* certainly has traits for tolerating higher environmental temperatures (Chapter 5), but does not exhibit any clear life history traits to make it a superior competitor (Chapter 6). This chapter attempts to detect the presence or absence of competition from adult size data, and experimentation. The experimental approach chosen was an additive design, where any negative effects on performance of the species infer that competition could possibly structure a community. The larval stage was chosen as the stage at which competition was most likely to take place. Larvae are confined in one dung pat until they have completed development. The larval food resource is expected to have a patchy distribution (Ives, 1991), therefore the *Philonthus*

distribution is likely to be aggregated in these patches (Keddy, 1989). If the females cannot assess the density of conspecific eggs, as in *Aphodius* species (Holter, 1979; 1982), then larvae of different species will be trapped together in the same dung pats, even if the adults exhibit density dependent emigration.

7.2 Methods

Evidence of competitive interactions between the three species of *Spatulonthus* was examined from two angles. Firstly, the morphology of the three species at the three different field sites was examined for evidence of competitive displacement or biotic release. Secondly, beetles were reared together in different combinations of species so that any direct effects of interference competition could be recorded.

7.2.1 Morphology

Hutchinsonian ratios are expected to be associated with a common resource that is possibly limited. All three species of *Spatulonthus* are generalist predators and as such, their diet will be influenced by the size of prey they can overpower. This in turn is assumed to be governed at least in part by the gape of the mandibles. As it proved impractical to measure mandible gape directly, the headwidth of the beetles was used as an indirect measure of how wide each beetle was able to open its mandibles. There are no apparent differences in the structure and use of the mandibles in these three species.

Headwidth was measured across the anterior margin of the eyes using an ocular micrometer on a Wild M3 dissection microscope. Headwidths were measured from all three, field-site populations of each species, and for populations reared in the laboratory at fixed temperatures (15 °C, 20 °C, 25 °C). The data sets for each species were tested for normality and ANOVA was used to test for intraspecific differences between populations, and interspecific differences within syntopic

populations. The variance of headwidths of each population of each species was used as an indication of the variance of the species. These values were subjected to an F-test (Levene's test of homogeneity of variances) to determine whether there were any differences in the variability of each species dependent on its site of origin.

7.2.2 Development

Adults of each species were collected from the Cluny farm field site. Pairs of beetles were kept in two-litre pots at 25 °C, as described in Chapter 2. Eggs were collected daily and placed individually in petri dishes. These were examined daily and the newly hatched first instar larva were placed into the two-litre pot rearing set-up, as described in Chapter 2. Larvae of the same age were reared in the following combinations.

Table 1 - Rearing combinations of three species of *Sparulonthus* larvae. All combinations were replicated x 20. Species A = *P. incognitus*; B = *P. labdanus*; C = *P. sanganus*.

Description	Number of larvae/pot	Combinations	
		Single species	Mixed Species
Singles	1	A; B; C	
Pairs	2	A + A; B + B; C + C	A + B; A + C; B + C
Trios	3	A + A + A; B + B +B; C + C + C	A + B + C

Performance was measured by comparing survival rates amongst the combinations. Each combination was replicated 20 times. *Musca domestica* eggs were provided daily as food, *ad libitum*, until all L3 had disappeared into the soil to pupate. Then the dung pat was replaced with a sponge, which was kept moist until the emergence of the adults about two weeks later. Survival and development time from egg to adult was recorded for each individual. Survival of

each species in mixed pair combinations and a mixed trio was compared by means of a Chi-squared test with a null hypothesis of no difference in survival of each species in the combination. Developmental times were compared within each species across all rearing combinations by ANOVA. Post hoc comparison of means was done with a Tukey HSD for unequal sample sizes (Spjotvoll/Stoline test; Statistica 1993).

7.3 Results

7.3.1 Morphology

Summary statistics for each species from each population, including a Kolmogorov Smirnov test for normality (D-statistic), are given in Table 2. Headwidths of all populations of all species were normally distributed. Sexual dimorphism in the field populations was only noted in the Cluny populations of *P. labdanus*, where the females are slightly larger, and the Cluny population of *P. sanamus* where the males are slightly larger (Table 3). Laboratory populations were not examined for sexual dimorphism.

Mean headwidths of each species were smaller in the field caught individuals as compared to the laboratory reared individuals (Fig. 1). No intraspecific differences were found in the field populations of any species, showing no evidence of biotic release in the absence (or at least severe reduction in numbers), of closely related competitors (Table 4).

Table 2. Summary statistics, and the results of a Kolmogorov Smirnov Test for normality, of the headwidth measures of three *Philonthus* species, field and laboratory populations.

Site / Species	n	Headwidth Mean ± SD	Minimum	Maximum	KS-D	P
Innisfree						
P. incognitus	54	0.83 ± 0.04	0.75	0.93	0.086	ns
P. labdanus	17	0.93 ± 0.04	0.87	1.03	0.120	ns
P. sanamus	90	0.98 ± 0.08	0.79	1.15	0.055	ns
Cluny						
P. incognitus	19	0.83 ± 0.03	0.78	0.87	0.187	ns
P. labdanus	65	0.97 ± 0.06	0.83	1.08	0.070	ns
P. sanamus	187	0.98 ± 0.08	0.80	1.20	0.067	ns
Boukenhouts						
P. incognitus	5	0.83 ± 0.08	0.76	0.97	0.237	ns
P. labdanus	7	0.94 ± 0.04	0.86	0.99	0.183	ns
P. sanamus	78	0.96 ± 0.08	0.79	1.16	0.071	ns
15 °C						
P. incogn	11	0.95 ± 0.03	0.89	0.99	0.111	ns
P. labd	23	0.99 ± 0.04	0.91	1.08	0.177	ns
P. sana	16	1.03 ± 0.07	0.94	1.2	0.117	ns
20 °C						
P. incognitus	18	0.97 ± 0.02	0.94	1.02	0.178	ns
P. labdanus	18	1.02 ± 0.04	0.94	1.08	0.160	ns
P. sanamus	21	1.12 ± 0.08	0.99	1.27	0.118	ns
25 °C						
P. incognitus	16	0.96 ± 0.03	0.90	1.00	0.192	ns
P. labdanus	24	1.04 ± 0.04	0.99	1.11	0.101	ns
P. sanamus	16	1.15 ± 0.10	1.02	1.32	0.150	ns

Table 3. Headwidth measurements (mean ± SD) of field populations of males and females of three *Philonthus* species, and results of Student's t-test for differences between sexes. - = too few individuals to measure.

Site / Species	Headwidth: Males (mm)			Females (mm)			Student's t-test		
	n	mean	SD	n	mean	SD	t	df	p
Innisfree									
P. incognitus	7	0.816	0.048	7	0.856	0.024	-1.992	12	0.070
P. labdanus	7	0.917	0.029	8	0.950	0.050	-1.511	13	0.155
P. sanamus	44	0.996	0.091	46	0.0973	0.071	1.372	88	0.174
Cluny									
P. incognitus	8	0.820	0.033	5	0.814	0.038	0.302	11	0.768
P. labdanus	32	0.948	0.056	28	0.990	0.055	-2.926	58	0.005
P. sanamus	89	1.003	0.092	98	0.964	0.05	3.547	185	0.001
Boekenhouts									
P. incognitus	-			-				-	
P. labdanus	4	0.960	0.038	3	0.913	0.046	1.468	5	0.202
P. sanamus	37	0.962	0.079	40	0.958	0.074	0.194	75	0.847

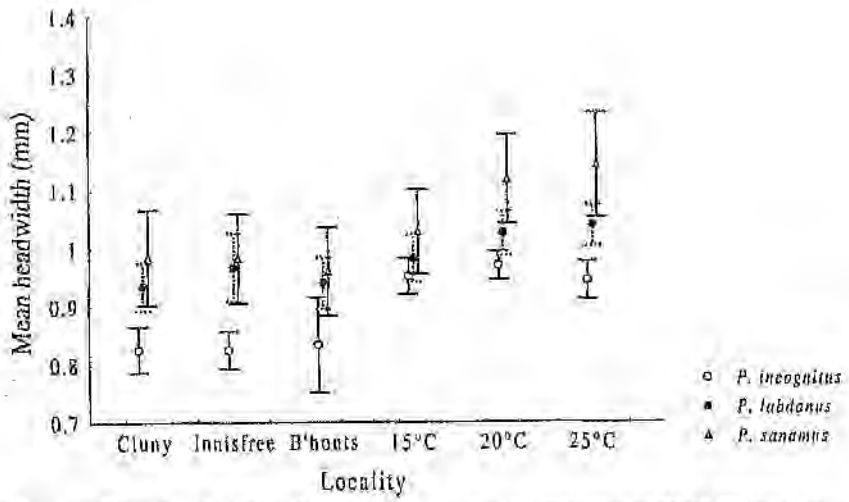


Figure 1. Mean headwidths of field and laboratory populations of three *Philonthus* species. (Error bars = 1SE).

Table 4. Intraspecific comparisons of headwidths of field populations of three *Philanthus* species.

Species		Tukey HSD P values	
P. incognitus	Site	Innisfree	Cluny
	Cluny	0.999	-
	Boekenhouts	0.951	0.945
	F (2,75) = 0.086 ; P = 0.916		
P. labdanus	Site	Innisfree	Cluny
	Cluny	0.189	-
	Boekenhouts	0.976	0.628
	F (2,86) = 2.890 ; P = 0.061		
P. sanamus	Site	Innisfree	Cluny
	Cluny	0.993	-
	Boekenhouts	0.141	0.171
	F (2,352) = 2.609 ; P = 0.075		

Interspecific comparisons of headwidths of field caught specimens showed *P. incognitus* to be significantly smaller than both *P. labdanus* and *P. sanamus* at all sites (Fig. 1; Table 5). The latter two species were found not to differ significantly in size (Table 5). The two larger species overlap almost completely in headwidth range in field populations (Fig. 2). No evidence of competitive character displacement was found as the variance of headwidth of each species did not differ significantly across sites (Table 6). Size ratios of the three species were fairly constant across sites (Table 7). The ratio of the smallest species to the two larger species was small, and the ratios between the larger two species were of the order of that found between sexes of the same species (Table 7).

Table 5. Interspecific comparisons of headwidths of field populations of three *Philonthus* species.

Site	Tukey HSD P Value		
Innisfree	Species	*P. incognitus*	*P. labdanus*
	P. labdanus	0.000	-
	P. sanamus	0.000	0.077
	F (2,158) = 94.062 ; P < 0.000		
Cluny	Species	*P. incognitus*	*P. labdanus*
	P. labdanus	0.000	-
	P. sanamus	0.000	0.436
	F (2,2268) = 42.472 ; P < 0.000		
Boekenhouts	Species	*P. incognitus*	*P. labdanus*
	P. labdanus	0.065	-
	P. sanamus	0.022	0.872
	F (2,87) = 6.903 ; P = 0.002		

Table 6. Variance of headwidths of field populations of three *Philonthus* species.

Species / Site	*P. incognitus*		*P. labdanus*		*P. sanamus*	
	n	variance	n	variance	n	variance
Innisfree	54	0.001562	17	0.001654	90	0.006694
Cluny	17	0.001055	65	0.003437	187	0.005994
Boekenhouts	5	0.006744	7	0.001969	78	0.005767
F test *	F (2,71) = 0.091; P = 0.763		F (2,86) = 1.954; P = 0.147		F (2,352) = 0.755; P = 0.470	

* Levene's test for homogeneity.

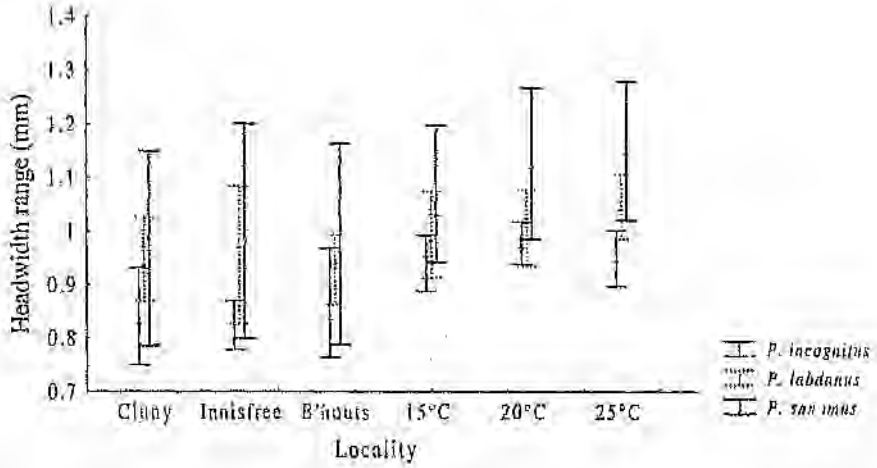


Figure 2. Headwidth ranges of field and laboratory populations of three *Philonthus* species. Range = maximum and minimum headwidths for each species.

Table 7. Ratios of mean headwidths of *Spatulonthus* species from three different field sites.

Species	Ratio
Site	
Innisfree	
P. incognitus/P. labdanus	1.13
P. incognitus/P. sanamus	1.19
P. labdanus/P. sanamus	1.05
Cluny	
P. incognitus/P. labdanus	1.17
P. incognitus/P. sanamus	1.19
P. labdanus/P. sanamus	1.02
Boekenhouts	
P. incognitus/P. labdanus	1.13
P. incognitus/P. sanamus	1.15
P. labdanus/P. sanamus	1.02

Headwidths of laboratory reared individuals are included for comparison with field caught material (Fig. 1). Species headwidths for all field sites were pooled.

Laboratory individuals are larger in all cases than field caught specimens, and increasing rearing temperature tends to increase the headwidth of emergent adults (Fig. 1; Table 8).

Table 8. Intraspecific comparison of headwidths of field and laboratory populations of three *Philonthus* species. (15 °C, 20 °C, 25 °C = rearing temperature)

Species		Tukey HSD P Value		
P. incognitus				
Site	Laboratory	Field	15 °C	20 °C
	15°C	0.000	-	-
	20 °C	0.000	0.670	-
	25 °C	0.000	0.949	0.188
		F (3,119) = 119.322 ; P < 0.001		
P. labdanus				
Site	Laboratory	Field	15 °C	20 °C
	15 °C	0.213	-	-
	20 °C	0.000	0.089	-
	25 °C	0.000	0.001	0.835
		F (3,150) = 22.01 ; P < 0.001		
P. sanamus				
Site	Laboratory	Field	15 °C	20 °C
	15 °C	0.261	-	-
	20 °C	0.000	0.006	-
	25 °C	0.000	0.000	0.503
		F (3,404) = 45.84 ; P < 0.001		

Variances of headwidths of laboratory reared beetles (Table 9) are similar to field collected material. *P. sanamus*, the largest species, is more variable, but there is not a markedly greater size range in the laboratory population of the smaller species which might be expected if their field counterparts were faring less well at the lower end of their size range. *P. sanamus* appear to be most favourably affected by higher temperatures, and this is reflected by the increase in the size ratios, as *P. sanamus* gets relatively larger than the other two species, and *P. labdanus* relatively smaller (Table 10).

Table 9. Variance of headwidths of laboratory populations of three *Philonthus* species

Species	*P. incognitus*		*P. labdanus*		*P. sanamus*	
Rearing temp. (°C)	n	variance	n	variance	n	variance
15	11	0.000967	23	0.001985	16	0.005321
20	18	0.000601	28	0.001310	21	0.005926
25	16	0.001027	24	0.001235	16	0.009[illegible]
F test *	F (2,42) = 0.707 P = 0.498		F (2,62) = 0.841 P = 0.436		F (2,50) = 1.573 P = 0.217	

* Levene's test for homogeneity.

Table 10. Ratios of the headwidths of three *Philonthus* species reared at three different temperatures.

Species	Ratio
15 °C	
P. incognitus/P. labdanus	1.04
P. incognitus/P. sanamus	1.08
P. labdanus/P. sanamus	1.04
20 °C	
P. incognitus/P. labdanus	1.05
P. incognitus/P. sanamus	1.15
P. labdanus/P. sanamus	1.09
25 °C	
P. incognitus/P. labdanus	1.08
P. incognitus/P. sanamus	1.19
P. labdanus/P. sanamus	1.11

7.3.2 Development

Survival rates of homogenous pairs of species and homogenous trios were compared with survival of beetles reared individually to check for intraspecific competitive effects, which were not found (Table 11). Mixed pairs and mixed trios were compared in the same way looking for interspecific competition. These effects were not found (Table 12).

Table 11. Chi-square results for intraspecific comparison of survival rates of three *Philonthus* species reared singly, in pairs, or in trios of the same species. (df = 1 in all cases)

Species	Comparison	x^2	P
P. incognitus	pairs vs singles	0.00	1
P. labdanus	pairs vs singles	0.4900	0.50<P<0.25
P. sanamus	pairs vs singles	0.7441	0.50<P<0.25
P. incognitus	trios vs singles	0.2300	0.75<P<0.50
P. labdanus	trios vs singles	0.0044	0.95<P<0.90
P. sanamus	trios vs singles	0.1141	0.75<P<0.50

Table 12. Chi-square results of survival rates of three *Philonthus* species reared in mixed combinations of individuals and species. (df = 1 in all cases).

Rearing combination	x^2	P
1 *P. incognitus* + 1 *P. labdanus*	1.125	0.75<P<0.50
1 *P. incognitus* + 1 *P. sanamus*	1.133	0.25<P<0.10
1 *P. labdanus* + 1 *P. sanamus*	0.000	P = 1
1 *P. incognitus* + 1 *P. labdanus* + 1 *P. sanamus*	0.153	0.75<P<0.50

Mean development times of larvae to adults, of the three species of *Philonthus* in various combinations of individuals are shown in Fig. 3. Significant effects of larval partners were found for all species (Table 13). Both *P. incognitus* and *P. labdanus* developed most quickly as conspecific pairs. This effect was not found

in *P. sanamus* cultures (Table 14). The presence of *P. sanamus* as a developmental partner had a detrimental effect in all combinations. When *P. sanamus* was paired with either *P. incognitus* or *P. labdanus*, their development was slowed to the equivalent of sharing the habitat with both other species. Development in a conspecific trio was significantly faster for *P. incognitus* and *P. labdanus* than in a mixed trio. However, this effect was not noted for *P. sanamus*. Clearly, the presence of *P. sanamus*, in whatever combination, has an effect of prolonging larval development of both conspecifics and other species.

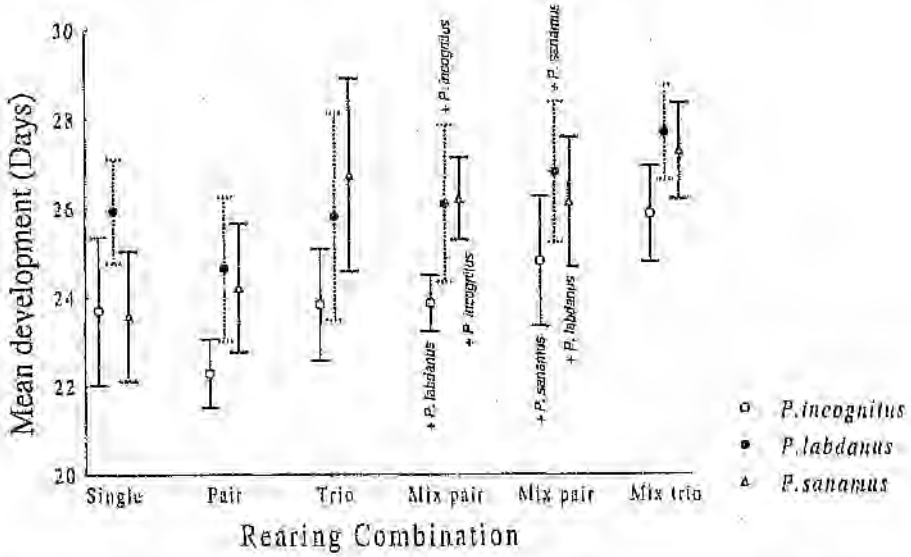


Figure 3. Development times (L1 - Adult) of three *Philanthus* species reared in different combinations. Singles, pairs and trios are conspecifics. Mixed pairs are as shown. Mixed trios are all species. (Error bars = 1SE).

Table 13. Mean developmental times (days) for three *Philonthus* species reared in various intra- and interspecific combinations. See Table 1 for description of combinations.

Species Combination	n	mean (days)
P. incognitus		
Single	16	23.68
Double	32	22.28
Trio	55	23.83
+ *P. labdanus*	15	23.86
+ *P. sanamus*	17	24.82
Mixed trio	18	25.88
P. labdanus		
Single	19	25.94
Double	31	24.64
Trio	55	25.81
+ *P. incognitus*	17	26.11
+ *P. sanamus*	18	26.83
Mixed trio	18	27.72
P. sanamus		
Single	17	23.58
Double	28	24.21
Trio	46	26.76
+ *P. incognitus*	13	26.23
+ *P. labdanus*	18	26.16
Mixed trio	16	27.31

Table 14. Intraspecific comparison of development times for three *Philonthus* species reared in various intra and interspecific combinations. See Table 1 for description of combinations. See Table 13 for developmental times.

Species	Tukey (HSD) P value				
P. incognitus					
Combination	Single	Pair	Trio	+ *P. labdanus*	+ *P. sanamus*
Pair	0.009	-	-	-	-
Trio	0.999	0.000	-	-	-
+ *P. labdanus*	0.998	0.032	1.000	-	-
+ *P. sanamus*	0.071	0.000	0.144	0.229	-
Mixed trio	0.000	0.000	0.000	0.000	0.090
	F (5,147) = 24.35 ; P < 0.001				
P. labdanus					
Combination	Solo	Pair	Trio	+*P. incognitus*	+ *P. sanamus*
Pair	0.241	-	-	-	-
Trio	0.999	0.117	-	-	-
+ *P. incognitus*	0.998	0.176	0.996	-	-
+ *P. sanamus*	0.695	0.045	0.556	0.835	-
Mixed trio	0.042	0.000	0.022	0.108	0.692
	F (5,152) = 7.43; P < 0.001				
P. sanamus					
Combination	Single	Pair	Trio	+*P. incognitus*	+ *P. labdanus*
Pair	0.884	-	-	-	-
Trio	0.000	0.009	-	-	-
+ *P. incognitus*	0.000	0.025	0.965	-	-
+ *P. labdanus*	0.000	0.005	0.893	0.999	-
Mixed trio	0.000	0.000	0.937	0.563	0.376
	F (5,132) = 17.06 ; P < 0.001				

7.4 Discussion

7.4.1 Morphology

The headwidths of the these individual *Spatulonthus* species are surprisingly uniform across the three field populations measured. Biotic release or character displacement was not seen as no major change or variation in the size of one or more species was found, despite the difference in abundance of the species at different sites. Classical Hutchinsonian ratios were also not found. In this regard the ghost of competition past was not glimpsed.

Because these three *Spatulonthus* species only represent a portion of the total *Philonthus* species inhabiting cow-dung pats on the highveld, it could be that other species replace the rare *P. incognitus* and *P. labdanus* at the Boekenhoutskloof site. Both species are cool adapted and may be physiologically restricted by the warmer conditions at Boekenhoutskloof. Nevertheless, it seems unlikely that a replacing species would fill the exact ecological space that *P. incognitus* and *P. labdanus* occupy without creating some effect on the size of all three *Spatulonthus* species. No obvious candidate for this role was noted in field collections. Gotelli (1997), found considerable overlap in the body size of coexisting ant lion species larvae, and concluded that traditional explanations of resource partitioning based on body size did not match his findings.

Significantly larger headwidths produced in laboratory cultures implies that *Spatulonthus* larvae developing in dung pats in the field are under some kind of stress which is sufficient to limit their adult headwidth to a size below its genotypic potential. This stress could be caused by adverse temperature, habitat destruction by scarabs, shortage of suitable prey, or competition from other *Spatulonthus*.

7.4.1.1 Developmental temperature - size rule.

An interesting result of this particular comparison of size in the study beetles is the effect of temperature on the size of emerging adults. There is a general increase in adult headwidth with temperature over the range shown, although *P. incognitus* are smaller at the highest temperature.

Intuitively, one expects that a higher temperature would result in a faster growth rate, producing bigger individuals with higher fecundity (Sibly and Atkinson, 1994). In reality, this assumption is not valid. Over 80% of ectotherms studied show exactly the opposite effect, a reduction in body size at maturity when reared at higher temperatures (Atkinson, 1994). This effect has been termed the developmental temperature-size rule (Atkinson and Sibly, 1997). There have been many attempts to explain this rule (Berrigan and Charnov, 1994; Ernsting, 1995; Perrin, 1995; Sevenster, 1995; Atkinson and Sibly, 1996) in terms of life history trade-offs or physiology. But what remains central to the issue is whether such a response is adaptive or simply a constraint (Partridge and Coyne, 1997). Evidence from low temperature experiments on *Drosophila* suggests that the rule effect is adaptive, and can be reversed in yellow dung flies dependent on the rearing temperature. (Blanckenhorn, 1997). However, Klingenberg and Spence (1997) found no correlation between female body size and performance in Gerrids.

Among the various intricate explanations of the reasons for the paradoxical smaller size of ectotherms reared at higher temperatures, some are physiological. For example, the rate of acquisition and anabolism of energy is relatively insensitive to temperature compared with catabolic rates (Atkinson, 1994; Perrin, 1995). Alternatively, resources (such as oxygen) may be reduced at higher temperatures, either limiting growth directly or selecting for the ability to mature earlier at higher temperatures before declining resources limit growth rate (Atkinson and Sibly, 1996), which would be expected to happen in the dung pat habitat. Other proposals centre on the effect of temperature on cell size. Usually

an increase in cell size is triggered by a low rearing temperature, which causes an increase in the final size of the whole organism (Partridge and French, 1996). In contrast, latitudinal comparisons revealed differences in body size that were associated with cell number rather than cell size (Atkinson and Sibly, 1997). This is explained by a model which assumes that the coefficient of growth rate is less than the coefficient of differentiation rate. Consequently, cells divide faster but grow proportionately less rapidly. An altitudinal cline in body size is predicted, which would be expected to parallel a latitudinal cline (Partridge and Coyne, 1997, although see Krasnov *et al.*, 1996). Again the results presented in this study differ in that no such cline was found.

Partridge and Coyne (1997) propose a life history trade-off when low temperatures increase larval mortality, selecting for reduced clutch size of improved quality, which in turn would increase the offspring's chances of survival. This effect was not found by Klingenberg and Spence (1997) in water striders, but has been shown in viviparous skinks (Rohr, 1997).

Whatever the reasons behind the developmental temperature - size rule, the three species of *Philonthus* examined in this study are one of the exceptions to it. This feature alone makes their developmental biology worthy of further investigation.

7.4.2 Development

Laboratory trials of competitive effects on different combinations of the three species did not reveal any intra- or interspecific effects on survival. Within the laboratory set-up cannibalism does not appear to take place. Presumably, the size differences between the developing larvae are not sufficient to allow *P. sanamus* in particular to easily prey on the other two species. However this assumption may not hold true as Gotelli (1997), found in contrast to most assemblages, that intraguild predation was greatest in animals of the similar size.

Competitive effects were found on the development times of the three species. These effects were marked and in the direction expected. For the first time in this study, results that go some way to explain the dominant abundance of *P. sanamus* were found. The presence of a *P. sanamus* larva in any of the cultures prolongs the development of any other larva that shares the experimental dung pat with it. This applies equally to conspecifics as to *P. incognitus* or *P. labdanus*. Interestingly, *P. sanamus* females were found to have a lower oviposition rate than the other two species (Chapter 6). *P. incognitus* exhibits a type of synergistic response in that two larvae of the same species per pat developed more quickly than a single larva.

Table 15 shows the maximum numbers of females of each species found in pats in the field. The average number of females of all occupied pats is 0.3 females/250g dung/2l pat. If each female lays eggs at a rate of three per day, this would result in, on average, one first instar larva having 250g of a dung pat to itself. Therefore, the laboratory density of three larvae/250g dung is high, more so when one considers that the laboratory set-up was essentially two dimensional, with little opportunity for larvae to move from the lower face of dung pat. The maximum of 21 females of all species found in one field pat would yield 7 - 9 eggs/250g dung which would clearly have an effect on the development of the species. The females' behaviour with regard to where and when she lays her eggs is obviously important in predicting the likelihood of *Spatulonthus* larvae experiencing some sort of competitive pressure. Female oviposition behaviour would be expected to be under the influence of a preference performance linkage (Price, 1995), with regard to prey density and numbers of potential competitors per pat. How she would assess the levels of these conflicting elements is unknown. Holter (1979), has shown *Aphodius* species to be unable to make this assessment. A long and futile attempt at washing *Spatulonthus* eggs out of field collected pats was unable

Table 15. Maximum number of females of three *Philonthus* species found in individual dung pats over a 12 month period. Species A = *P. incognitus*; B = *P. labdanus*; C = *P. sanamus*.

	Maxi . n number of females in a single dung pat											
Date	March '90			April '90			May '90			June '90		
Species / Locality	A	B	C	A	B	C	A	B	C	A	B	C
Innisfree	1	0	1	0	2	4	1*	0	1*	1*	0	1*
Cluny	1*	3*	5*	3*	4*	14*	0	1*	1*	0	0	1
Boekenhouts	0	1	0	1*	1*	4	0	0	4	0	0	1
Date	July '90			August '90			September '90			October '90		
Species / Locality	A	B	C	A	B	C	A	B	C	A	B	C
Innisfree	1*	0	1*	0	0	1	1*	1*	4	0	1	1
Cluny	0	1	0	9	0	1	1	1*	6	0	1	0
Boekenhouts	0	0	2	0	0	17	0	0	6	0	0	7
Date	November '90			December '90			January '91			February '91		
Species / Locality	A	B	C	A	B	C	A	B	C	A	B	C
Innisfree	2	0	1	1	0	1	0	4	0	6*	1*	1*
Cluny	1*	1*	13*	0	1	1	1#	2*	1*	0	1	1
Boekenhouts	1*	0	4*	1*	0	2*	0	0	1	1	0	2

Table legend:
* Species sharing the same pat
\+ Sharing pat with 1 *P. labdanus* and 4 *P. sanamus*
\# Sharing pat with 1 *P. labdanus*

to cast any light on this subject in this study. Alternatively larvae of the different species could be extracted from field collected pats to discover if all three species are actually breeding in the same pats at the same time. Unfortunately the larvae

do not leave the pats in Berlese funnels as readily as the adults do, which will create conditions for predation and cannibalism, biasing the results obtained.

7.4.3 Conclusion

Philonthus sanamus, with its competitive larvae, and tolerance of higher temperatures now starts to fulfil some expectations of superior competitor. Slightly larger and more abundant than the other two species, it has both the characteristics considered to be indicative of a dominant competitor; it suppresses the other species and can tolerate the environment better (Kreddy, 1989).

Given the evenness of the species' headwidths across the three field sites, the laboratory derived headwidth data provides interesting and confusing possibilities. Firstly, that *P. sanamus* is most favourably influenced by elevated developmental temperatures as it increases the adult size over the range tested. In contrast, *P. incognitus*, is smaller when reared at 25 °C. These data support the conclusion that the former species is adapted to a warmer climate than the latter. However, the result that the field caught specimens of all species were smaller than their laboratory reared counterparts indicates that, contrary to earlier assumptions (Chapter 4), resources are limited in some form for most individuals. Time as the pat dries out, and or food, are the most obvious candidates for the limited resources, and this will most probably bring developing larvae into a competitive situation with each other. From anecdotal observations made during the course of this study it is suspected that the experimental beetles can shorten their normal development and pupate at an earlier stage and smaller size than their genotypic potential. Plasticity of adult sizes is seen in dung scarabs in response to varying food availability (Emlen, 1994; 1997, Hunt and Simmons, 1997), and this type of reaction norm is not surprising in animals that develop in such an ephemeral habitat as dung.

CHAPTER EIGHT

8.1 Concluding remarks

Finally, having reached a point at which competition and its effects have been directly and indirectly measured, there appears to be no mechanism shared by these species for avoiding that competition, other than the stochastic process of finding suitable dung pats. Ultimately, the expectation of character displacement of any nature may be an unrealistic expectation. Species have to coexist if they are to co-evolve and an increase in the total number of consumers in a habitat will decrease resource densities. Under these conditions, consumers should generalise in their foraging, which could cause an increase in similarity (Abrams, 1990). Depending on the nature of the consumer and resource dynamics, evolutionary and ecological effects of competition are not likely to result in evenly-spaced resource utilisation characteristics or morphologies (Abrams, 1990).

To the best of our knowledge, all organisms are limited to some extent in their spatial distribution on the earth's surface. The size of these distributions varies widely, and often the cause of the limits to species range are not obvious or well understood. One of two groups of opposing hypotheses is usually invoked to explain why animals live where they do. The "Ecological, full-world model" (Alexander, 1996), or "Equilibrium paradigm" (Simberloff, 1982) assumes habitats saturated with species, close to the maximum number that can coexist in any place. They predict the events of community succession, and emphasise that communities are closed assemblages of species that are tightly linked and highly coevolved. This static community model predicts that communities are stable through geologic time (Graham, 1986; Graham and Grimm, 1990), and that biotic factors, particularly interspecific competition are of overriding importance in dictating who is a community member (Walter and Paterson, 1994). The alternative hypotheses are the "Historical, speciation-driven model", or Non-equilibrium paradigm (Pickett *et*

al., 1992; Reice, 1994; Rohde 1997), where the world is not full, but continually responding to disruption from a wide range of forces or events. In this view communities are loosely organised collections of species whose coexistence is largely a result of chance and abiotic factors. Environmental changes cause individual species to respond and form new species associations (Graham and Grimm, 1990) which may not be constant through time. Therefore, modern communities may be less than 10,000 years old and shaped largely by abiotic forces, which impinge on the physiology of species.

From the evidence presented in the course of this study, the characteristics of each species measured bear little evidence of the presence or absence of their closest relatives and potential competitors. No mechanisms of coexistence were found and the conclusion is reached that for the dung-dwelling *Spatulonthus* at least, the community is not a "full-world".

Appendix

Material studied to generate the distribution maps presented in Chapter 4. Acronyms used:- British Natural History Museum, London, BMNH; Transvaal Museum, Pretoria TM; South African Museum, Cape Town, SAM; Personal collection, WITS. Contractions used:- Doctor, Dr; farm, frm; forest, for; forest station, for st; miles, mls; nature reserve, nat res; near, nr; Transvaal, Tvl;.

Table 1. Locality data for *P. incognitus* (Details in square brackets are added)

Museum	Locality	Coordinates	Date	Collector
	Ethiopia			
BMNH	Abyssinia, Mount Chillalo. 1200 -1300ft.	7.42N 39.22E	21/11/1926	Dr H. Scott
BMNH	Abyssinia, between Djem-Djem and Wourambouichi, 8000 - 9000ft	N.F.	30/9/1926 and 1/10/1926	Dr H. Scott
BMNH	Abyssinia, Wachacha Ravine nr Addis Abeba c8000ft	9.03N 38.4E	9/9/1926	Dr H Scott
BMNH	Abyssinia, Wourambouichi, Serpent Lake	N.F.	2/10/1926	Jomar-Caspar
BMNH	Ethiopia, Simien nr Mindigabsa, c.10000 ft.	N.F.	29/12/1952	Dr H. Scott
BMNH	Ethiopa, Simien Mai Datcha, E. of Arcuasie c.13200 ft.	14.99N 37.50E	5/12/1952	Dr H. Scott
BMNH	Abyssinia, Gamo Prov. Chencha, (8,900 ft).	N.F.	26/11/1948	Dr H. Scott
	Kenya			
BMNH	[Kenya], Naivasha	0.443S 36.26E	/7/1937	H.J.A. Turner
	South Africa			
TM	S Africa, Natal Midlands, Karkloof for 1300m.	29.18S 30.13E		S. Endrödy-Younga
TM	S Africa, Golden Gate, GGHNP Survey	28.65S 28.75E	25/1/1968	Potgieter and Jones
TM	S Africa, Cathedral Peak E-Y 1286	28.57S 29.12E	10/11/76	C. Scholtz
TM	S Africa, Manyeleti Game Reserve	24.36S 31.27E		S. Endrödy-Younga
TM	S Africa, Cape Prov. Marathon E-Y	34.02S 23.19E		S. Endrödy-Younga
TM	S Africa, Cape Mts. Baviaanskloof	33.36S 24.23E		S. Endrödy-Younga

Museum	Locality	Coordinates	Date	Collector
TM	S Africa, Swartberge, Blesberg West. 1820m E-Y1536	33.25S 2.40E		S. Endrödy-Younga
TM	S Africa, Cape Amatole, Isidenge for st	34.41S (sic) 27.15E		S. Endrödy-Younga
TM	S Africa, E.Tvl Klaseri E-Y 1769	23.59S 31.02E		S. Endrödy-Younga
TM	S Africa, E. Tvl Uitsoek. High altitude grass E-Y 2296	25.15S 30.34E		S. Endrödy-Younga
TM	S Africa, Tvl Nelshoogte for st E-Y2349	25.50S 30.50E		S. Endrödy-Younga
TM	S Africa, SW Cape. Gansbaai E-Y1744	34.35S 19.21E		S. Endrödy-Younga
TM	S Africa, Uitsoek. Grootkloof Ind. for E-Y2395	25.15S 30.33E		S. Endrödy-Younga
TM	S Africa, Nascott GR E-Y2571	25.54S 29.40E		
TM	S Africa, Nelshoogte. Knuckles Grassveld E-Y2442	25.47D 30.49E		S. Endrödy-Younga
TM	S Africa, Swartberge Blesberge W 1820m E-Y1535			
TM	S Africa, Natal, Weza. Impetyene Grassveld E-Y2678	30.37S 29.42E		S. Endrödy-Younga
TM	S Africa, W. Cape Nuweberg Camp E-Y244	34.03S 19.04E		S. Endrödy-Younga
TM	S Africa, Natal Middld. Karkloof Grassveld E-Y2735	29.19S 30.15E		S. Endrödy-Younga
TM	S Africa, SW Cape Hanequas Mt. 1350m E-Y1520	33.40S 19.05E		S. Endrödy-Younga
TM	S Africa, E. Tvl Berlin Forest E-Y2417	25.33S 30.44E		S. Endrödy-Younga
TM	S Africa Tvl Klaserie E-Y1769	23.59S 31.02E		S. Endrödy-Younga
WITS	S Africa, Tvl Inni ;free frm nr Sandton	26.06S 28.04E		M.J.Byrne
WITS	S Africa, Tvl Cluny frm nr Kyalami	25.57S 28.03E		M.J. Byrne

Museum	Locality	Coordinates	Date	Collector
WITS	S Africa, Boukenhouts frm nr Roodeplaat Dam	25.33S 28.27E		M.J.Byrne

Table 2. Locality data for *P. labdanus*. Locality data for *P. labdanus* and *P. maskinius* have been combined, see chapter 4. (Details in square brackets have been added).

Museum	Locality	Coordinates	Date	Collector
	Angola			
BMNH	Angola, Tundavala, 8-10 mls NW Sa da Bandeira.	14.50S 13.25E	2?/2/1972	P. Hammond
BMNH	Angola, Chibemba.	15.45S 14.05E	22/2/1972	P. Hammond
	Ethiopia			
BMNH	Abyssinia, Djem Djem Forest	NF	9/1926	J. Omer-Cooper
BMNH	Abyssinia, Mt. Chillalo, c10,000ft	7.42N 39.22E	17/11/1926	H. Scott
BMNH	Abyssinia, Mt. Zuquala c9000ft.	NF	25/10/1926	Dr H. Scott
	Kenya			
BMNH	[Kenya] Muguga	1.12S 36.38E	1/5/1954	V.F. Eastop
BMNH	[Kenya] Thika Rd.	1.03S 37.05E	30/6/1954	V.F. Eastop
	Namibia			
BMNH	SW Africa, Rietfontein, 23 mls SW Grootfontein	19.05S 17.52E	3/4/1972	P. Hammond
BMNH	SW Africa, Onguma Fm 55 mls NW Tsumeb	18.53S 16.59E	19/2/1972	P. Hammond
	Nigeria			
BMNH	Bamenda, [Nigeria]	NF	28/1/1952	V.F. Eastop
	South Africa			
BMNH	S Africa, Little Falls, 20 mls NW Johannesburg	26.07S 27.53E	6/5/1972	P. Hammond
BMNH	[S Africa] Johannesburg, Park Lake?	26.10S 28.02E	3/3/1932	A.M. Airson
BMNH	S Africa, 15 mls SW Johannesburg.	26.21S 27.53E	28/12/1971	P. Hammond
BMNH	S Africa, 5 mls SW Citrusdal.	32.40S 18.57E	6/1/1972	P. Hammond
BMNH	Botswana, 2 mls N Gweta	20.11S 25.15E	2/4/1972	P. Hammond

Museum	Locality	Coordinates	Date	Collector
BMNH	S Africa, Natal Hluhluwe Game Reserve	28.01S 32.18E	2/2/1986	C. Fox
TM	S Africa, Natal Middld., Karkloof for 1300m	29.18S 30.13E		S. Endrödy-Younga
TM	S Africa, Cape Prov., George Saasveld	33.57S 22.30E		Breyten-Dach
TM	S Africa, Cape Prov., Marathon	34.02S 23.19E		S. Endrödy-Younga
TM	S Africa, SW Cape, Bains Kloof	33.30S 19.10E		S. Endrödy-Younga
TM	S Africa, Cape, Matjiesfontein	33.16S 20.30E		S. Endrödy-Younga
TM	S Africa, E.Tvl., Berlin, Karstplat E-Y2375			S. Endrödy-Younga
TM	S Africa, Swartberge, Blesberg W, 1850m E-Y1537	33.24S 22.40E		S. Endrödy-Younga
TM	S Africa, Tvl Blyderiver E-Y1766	24.35S 30.49E		S. Endrödy-Younga
TM	S Africa, Natal, Cathedral Peak E-Y1075	28.57S 29.12E		S. Endrödy-Younga
TM	S Africa, Natal, Impetyene Grassveld E-Y2680	30.37S 29.42E		S. Endrödy-Younga
TM	S Africa, S.Cape, Tsitsikama Lottering	33.56S 23.40E		S. Endrödy-Younga
TM	S Africa, E.Tvl Uitsoek High Alt. Grassveld E-Y2296	22.15S 30.34E		S. Endrödy-Younga
TM	S Africa, Cape Karoo, Zwartskraal Farm E-Y539	33.10S 22.32E		S. Endrödy-Younga
TM	S Africa, Tvl Nelshoogte, Knuckles Rock Farm E-Y2310	25.47S 30.50E		S. Endrödy-Younga
SAM	S Africa, SW Cape, Waylands frm nr Darling	33.24S 18.26E	7/8/87	A. Davis
WITS	S Africa, Tvl Innisfree frm nr Sandton	26.06S 28.04E		M.J.Byrne
WITS	S Africa, Tvl Cluny frm nr Kyalami	25.57S 28.03E		M.J. Byrne
WITS	S Africa, Boukenhoutskloof frm nr Roodeplaat Dam	25.33S 28.27E		M.J.Byrne

Museum	Locality	Coordinates	Date	Collector
	Sudan			
BMNH	[Sudan] Bahr el Ghazal Prov.	8.30N 28.30E		
	Zimbabwe			
BMNH	Rhodesia, Wankie Game Reserve		1/10/1959	J.C. Wie

Table 3. Locality data for *P. sanamus*. Details in [square brackets added].

Museum	Locality	Coordinates	Date	Collector
	Angola			
BMNH	Angola, nr Luimbale, 12 mls SW c5500ft	12.21S 15.11E	21/3/1972	P. Hammond
BMNH	Angola [A33] Novo Redondo, 30 mls S	11.36S 14.00E	19/3/1972	P. Hammond
BMNH	Angola, Rocadas, R. Cunene	16.43S 14.56E	22/2/1972	P. Hammond
BMNH	Angola, Bruco	15.02S 13.13E	26/2-2/3/1972	P. Hammond
BMNH	Angola (A4) Chibemba	15.45S 14.05E	22/2/1972	P. Hammond
	Botswana			
BMNH	Botswana, Moremi Reserve	19.25S 23.40E	20/4/1972	P. Hammond
BMNH	Botswana, 10 mls W Mosetse	20.38S 26.32E	24/4/1972	P. Hammond
BMNH	Botswana, Francistown, 37 mls S	21.37S 27.21E	25/4/1972	P. Hammond
BMNH	Botswana, L. Ngami, 12 mls NE Sehitwa	20.23S 22.53E	17/4/1972	P. Hammond
	Ethiopia			
BMNH	Samara [Ethiopa]	12.00N 38.50E	13/8/1956	V.F. Eastop
BMNH	Hartau Br. Somaliland	NF	?	?
BMNH	Dolphin B. Br Somaliland	NF	?	?
	Kenya			
BMNH	Muguga (Kenya)	1.12S 36.38E	13/10/1953	V.F. Eastop
BMNH	Pietersburg 22km N	28.02S 23.17E	22/2/1986	C. Fox
	Namibia			
BMNH	SW Africa, Rietfontein, 23mls SW Grootfontein	19.50S 17.52E	3/4/1972	P. Hammond
BMNH	SW Africa, nr Karibib	21.50S 15.36E	31/1 - 2/2/1972	P. Hammond
BMNH	SW Africa, Onguma frm55 mls NW Tsumeb [W43]	18.53S 16.58E	19/2/1972	P. Hammond

Museum	Locality	Coordinates		Date	Collector
BMNH	SW Africa, [W36] Otjikoko Sud fr.., 33 mls ENE Omaruru	21.17S	16.27E	13/2/1972	P. Hammond
BMNH	Regenstein (SW Africa) 15 mls SSW Windhoek	22.34S	17.0oE	8/11/1972	P. Hammond
TM	SW Africa, Kungveld, Botswana Border EY1452	20.07S	21.00E		S. Endrödy-Younga
BMNH	SW Africa, Kahn River	21.53S	15.33E	31/1/1972	P. Hammond
	Nigeria				
BMNH	Bauchi (Nigeria)	10.16N	9.50E	24/10/1956	V.F. Eastop
	South Africa				
BMNH	Kimberley (S. Africa)	28.45S	24.46E		R.J. Power
BMNH	Pretoria (S Africa)	25.45S	28.12E	23/1/1928	
BMNH	Aliwal North (S Africa)	30.42S	26.43E	/12/1922	R.E. Turner
BMNH	S Africa 5 mls SW Citrusdal	32.40S	18.57E	6/1/1972	P. Hammond
BMNH	S Africa, Tom Burke, Tvl.	23.04S	28.00E	26/4/1972	P. Hammond
TM	SW Africa, Komashochl f.m Hochenheim EY 552	23.20S	16.20E		S. Endrödy-Younga
TM	S Africa, N.Tvl Mmabolela Estate	24.40S	28.15E		S. Endrödy-Younga
TM	SW Cape, Bains Kloof EY220	33.30S	19.10E		S. Endrödy-Younga
TM	S Africa, NW Tvl Ellisras EY340	23.40S	27.45E		S. Endrödy-Younga
TM	S Africa, Bushmanland, Pofadder 20km N EY1242	29.01S	19.27E		S. Endrödy-Younga
TM	Transkei, Dwesa Settlement EY2164	32.15S	28.49E		S. Endrödy-Younga
TM	S Africa, Dukuduku for sta EY334	28.22S	32.19E		S. Endrödy-Younga
TM	S Africa Tvl Nelshoogte for sta EY2348	25.50S	30.50E		S. Endrödy-Younga
TM	S Africa, Richtersveld frm. Harambeep	29.06S	18.40E		S. Endrödy-Younga
SAM	Redlingshuis (GC-170-12)	NF		Sept 1977	A.J. Prins
SAM	ElandsBay (GC-350-13)	NF		June 1979	A.J. Prins
SAM	S Africa, Tvl Blyde River Canyon	24.35S	30.49E	28/11/1991	F. Gewier
SAM	S Africa, Tvl Nylsvley Hill Base	24.40S	28.42E		S. Endrödy-Younga

Museum	Locality	Coordinates	Date	Collector
SAM	S Africa, Tvl Innisfree frm nr Sandton	26.06S 28.04E		M.J. Byrne
SAM	S Africa, Tvl Cluny frm nr Kyalami	25.57S 28.03E		M.J. Byrne
SAM	S Africa, Tvl Boukenhoutskloof frm nr Roodeplaat	25.33S 28.27E		M.J. Byrne
SAM	S Africa, SW Cape, Oranjefontein frm nr Darling	33.25S 18.26E	7/8/1987	A. Davis
SAM	S Africa, SW Cape, Pampoenvlei frm nr Darling	33.28S 18.24E	7/8/1987	A. Davis
SAM	S Africa, SW Cape, Good Hope nat res	34.18S 18.27E	7/8/1987	
SAM	S Africa, SW Cape, Groote Post frm nr Darling	33.26S 18.25E	7/8/1987	A. Davis
SAM	S Africa, SW Cape, Bon Attente frm nr Simonstown	34.15S 18.28	7/8/1987	A. Davis
SAM	[S Africa, Cape] Heidelberg (GC-268-14)	34.05S 20.57E	Oct.1978	A.J. Prins
SAM	[S Africa, Cape] Elim (GC-130-25)	34.36S 19.45E	June 1977	A.J. Prins
SAM	[S Africa] SW Cape, Waylands frm nr Darling	33.24S 18.26E	10/11/1987	A. Davis
SAM	[S Africa] SW Cape, West Coast National Park	33.10S 18.08E	10/11/1987	A. Davis
SAM	[S Africa] SW Cape, Groote Pst frm nr Darling	33.26S 18.25E	10/11/1987	A. Davis
SAM	[S Africa] SW Cape, Mooderrivier frm nr Atlantis	33.28S 18.20E	10/11/1987	A. Davis
SAM	[S Africa] SW Cape, Pampoenvlei frm nr Darling	33.28S 18.24E	10/11/1987	A. Davis
SAM	[S Africa] Montagu [GC-111-17]	33.47S 20.07E	March 1977	A.J. Prins
SAM	[S Africa] Malmesbury [GC-201-21]	33.28S 18.43E	Dec 1977	A.J. Prins
SAM	[S Africa] Still Bay [GC316-32]	34.23S 21.24E	March 1979	A.J. Prins

Museum	Locality	Coordinates		Date	Collector
SAM	[S Africa] Elim [GC-130-25]	34.36S	19.45E	June 1977	A.J. Prins
SAM	[S Africa] Heidelberg (GC-268-14)	34.05S	20.57E	Oct 1978	A.J. Prins
SAM	[S Africa] C.Tvl Nascott GR EY2568	25.54S	29.40E		S. Endrödy-Younga
SAM	S Africa, SW Cape, Oranjefontein frm nr Darling	33.25S	18.26E	7/8/1987	A. Davis
SAM	S Africa, SW Cape, Pampoenvlei frm nr Darling	33.28S	18.24E	7/8/1987	A. Davis
SAM	S Africa, SW Cape, Good Hope nat res	34.18S	18.27E	7/8/1987	A. Davis
SAM	S Africa, SW Cape, Groote Post frm nr Darling	33.26S	18.25E	7/8/1987	A. Davis
SAM	S Africa, SW Cape, Bon Attente frm nr Simonstown	34.15S	18.28E	7/8/1987	A. Davis
SAM	[S Africa Cape] Heidelberg (GC-268-14)	34.05S	20.57E	/10/1978	A.J. Prins
SAM	[S Africa, Cape] Elim (GC-130-25)	34.36S	19.45E	/6/1977	A.J. Prins
WITS	S Africa, Tvl Innisfree frm nr Sandton	26.06S	28.04E		M. Byrn
WITS	S Africa, Tvl Cluny frm nr Kyalami	25.57S	28.03E		M. Byrne
WITS	S Africa, Tvl Boukenhouts Kloof frm nr Roodeplaat Dam	25.33S	28.27E		M. Byrne
	Tanzania				
BMNH	Amani (Tanzania)	5.09S	38.36E	31/1/1955	V.F. Eastop

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