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Aspects of Temporal Resource Partitioning among Dung Beetles (Coleoptera: Scarabaeidae) of the Kizilirmak Delta on the Black Sea Coast of Turkey

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Scarabaeus sacer L.

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Abstract

Local assemblages of dung beetles in natural and altered ecosystems worldwide contribute to a suite of ecological functions and ecosystem services, including bioturbation and pest and parasite suppression. There is generally a strong competitive hierarchy for the dung resource among the three main guilds or functional groups of dung beetle species, with ball rollers more competitive than tunnellers, and tunnellers more competitive than dung dwellers.

How are inferior competitors able to co-occur or coexist with superior competitors? Temporal resource partitioning is one of the mechanisms that can facilitate co-occurrence and coexistence in local assemblages. The primary purpose of this study was to investigate if, and how, temporal resource partitioning manifests at the interspecific, intraguild and interguild levels in a warm, temperate climate assemblage of dung beetles (Coleoptera: Scarabaeidae; Aphodiinae, Scarabaeinae) in the Kizilirmak Delta on the central Black Sea coast of northern Turkey.

Twenty three species of dung beetles in three guilds were recorded in a seasonal survey of natural dung pads in 2013. In the summer of 2014, the effects of dung pad size on ball production by the large dung ball roller, *Scarabaeus sacer* (L.) were investigated with standardised dung pads. Ball production by *S. sacer* was concentrated on a small number of pads of the three largest sizes. Ball size increased but the number of balls produced per 100 g of dung decreased with increasing pad size. Ball production and time of day were significantly related ($P < 0.01$).

In the summers of 2014 and 2015, standardised dung pads were used in two field experiments at the same site that investigated the effects of dung pad deposition time and exposure period, and their interaction, on species richness, abundance and biomass. During the experiments, an additional four dung beetle species were collected, bringing the total number to 27 species that included one ball rolling, 17 dung dwelling and nine tunnelling species. The large ball roller, *S. sacer* L., and small and medium-sized tunnellers, dominated assemblages in the first 24 h but they were then superseded by dwellers. Succession was highly compressed, with maximum abundance at 12 h and maximum species richness at 24 h. Regression analysis demonstrated a significant relationship ($P < 0.01$) between species richness and the inverse of the Berger-Parker dominance index (d); i.e., as the number of species increased, the abundance of individual species became more even.

In addition, ANOVA was used to model the temporal dung use patterns of the dwelling and tunnelling guilds and correlation analysis was used to determine the interspecific and interguild relationships that underpin those patterns. ANOVA revealed significant effects of dung deposition time, dung exposure period, and their interaction, on the mean abundance of guilds. The tunnelling species appear to have been aggregated firstly by relatively synchronous diel activity and then by habitat filtering along the gradient of decreasing moisture content. 'Limiting similarity', which postulates that competitive exclusion limits the coexistence of taxa that are too similar in their traits, appears to have then restricted the number of tunnelling species that could be both concurrent and abundant. Conversely, dung dwelling species dispersed relatively uniformly across the six dung deposition times which meant they were able to exploit 'temporal refuges', i.e., dung pads with lower densities of tunnelling species which are generally superior competitors. Furthermore, both these guilds were most active during periods that reduced the potential for competition with the dominant competitor *S. sacer*, which was most active in the late dusk and early night.

Separately, the patterns of interspecific, intraguild and interguild association or aggregation were investigated with correlation analysis to better understand their potential role in temporal resource partitioning. The general pattern of correlations was consistent between 2014 and 2015, with strong, positive correlations between the tunnelling species, low correlations between tunnelling and dung dwelling species, and low correlations between the dung dwelling species. This pattern of correlations indicated that temporal separation, and by inference, temporal resource partitioning, was occurring between the dung dwelling and tunnelling guilds. The mostly strong associations between tunnelling species may have reflected higher levels of negative, intraspecific interactions than negative, interspecific interactions, and similar competitive abilities.

The generally strong, congeneric aggregation of the tunnelling *Onthophagus* spp. and *Euoniticellus* spp. may lend support to contemporary coexistence theory's contention that increasing phylogenetic proximity, or relatedness, does not necessarily lead to competitive exclusion. Overall, the results of this study suggest that its methodology, supplemented by additional temporal and spatial experiments, can provide even deeper insights into the mechanisms underpinning the co-occurrence and coexistence of dung beetles, other dung fauna, fauna in other ephemeral resource patches, and insect faunas in general.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly authored works that I have included in my thesis. I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award. I acknowledge that an electronic copy of my thesis must be lodged with the University Library and, subject to the policy and procedures of The University of Queensland, the thesis be made available for research and study in accordance with the Copyright Act 1968, unless a period of embargo has been approved by the Dean of the Graduate School. I acknowledge that copyright of all material contained in my thesis resides with the copyright holder(s) of that material. Where appropriate, I have obtained copyright permission from the copyright holder to reproduce material in this thesis.

Publications during candidature

Journal publications

Sullivan G T, Ozman-Sullivan S K, Lumaret J-P, Bourne A, Zeybekoglu U, Zalucki M P, Baxter G. 2017. How guilds build success; aspects of temporal resource partitioning in a warm, temperate climate assemblage of dung beetles (Coleoptera: Scarabaeidae). Environmental Entomology, 46: 1060-1069. doi: 10.1093/ee/nvx117

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Tixier T, Lumaret J-P, **Sullivan G T**. 2015. Contribution of the timing of the successive waves of insect colonisation to dung removal in a grazed agro-ecosystem. European Journal of Soil Biology, 69: 88-93.

Conference paper

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Conference abstracts

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Sullivan G T, Ozman-Sullivan S K, Bourne A, Lumaret J-P, Zeybekoglu U, Zalucki M P, Baxter G. 2016. Succession patterns in a warm, temperate-climate assemblage of coprophagous dung beetles (Coleoptera: Scarabaeidae) in Turkey. VI Turkish Plant Protection Congress with International Participation, 5-8 September 2016, Konya, Turkey, p. 233.

Sullivan G T, Ozman-Sullivan S K, Bourne A, Lumaret J-P, Zeybekoglu U, Zalucki M P, Baxter G. 2016. Aggregation and resource partitioning by dung beetles (Coleoptera: Scarabaeidae). VI Turkish Plant Protection Congress with International Participation, 5-8 September 2016, Konya, Turkey, p. 411.

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Contributor	Statement of contribution
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Co-occurrence, correlation coefficient, diel separation, dung beetle, guild, interspecific competition, limiting similarity, *Scarabaeus sacer*, seasonal, resource partitioning

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CHAPTER 1 Introduction to the study

1.1 Background

Ephemeral resource patches include animal dung pads, leaf packs in streams, fruits, mushrooms and carrion (Finn 2001). Mohr (1943) described dung pads as scattered microhabitats of high quality resources of relatively small size and short existence that support complex communities. Dung composition, which is dependent on the producers, namely herbivores (ruminants and non-ruminants, including producers of pelleted dung), omnivores and carnivores, influences community composition (Doube 1991; Filgueiras et al. 2009; Whipple 2011). The physical and chemical composition of dung changes over time, e.g., there are reductions in the moisture content (Lumaret 1995), nitrogen content Holter (2016), emission rate of volatile compounds (Dormont et al. 2007), and dry dung mass (Tixier et al. 2015), causing a continuously changing dung environment (see also section 1.4.5). The most obvious group of dung users are the insects, with 26 families of coprophages, mycophages, saprophages, predators and parasitoids reported by Hanski (1991a). However, dung is also used as a resource by other groups, including mites (Hartini et al. 2009; Ozman-Sullivan et al. 2014), annelids (Tixier et al. 2015) and non-fauna organisms, including fungi (Dix and Webster 1995). Earlier colonisers of a pad can precondition it for further colonisation and thus influence the later structure of the community (Valiela 1974). Furthermore, Connell and Slayter (1977) stated that facilitation can occur during the process of heterotrophic succession. However, in some environments, especially tropical environments, ball rolling and large tunnelling dung beetles can decimate a pad in a short period (Anderson and Coe 1974; Krell-Westerwalbesloh et al. 2004). For a detailed discussion of temporal succession in dung beetle communities in temperate and tropical environments, see Krell-Westerwalbesloh et al. (2004).

Dung beetles (Coleoptera: Geotrupidae, Scarabaeidae) can be found in most environments from the tropics to the coolest temperate regions and up to 5,000 m altitude (Doube 1991; Lumaret and Stiernet 1991, 1994; Boonrotpong 2012). They provide a suite of essential ecological functions and ecosystem services such as dung degradation, bioturbation, secondary seed dispersal, and reduction in the numbers of pests and parasites of humans and domestic animals, and have been used as indicator species in natural and altered ecosystems across their range (Nichols et al. 2008).

Furthermore, Lumaret et al. (1992) reported that species richness increases the ability of a community to respond to changing environmental circumstances. As species respond differently to disturbance (Hooper et al., 2005), the benefits of higher biodiversity in maintaining functioning can become more obvious after perturbation (Hooper et al., 2005; Beynon et al. 2012). It is therefore essential that all aspects of the ecology of local and regional assemblages of dung beetles continue to be investigated so that their contributions to ecological functions and ecosystem services (Nichols et al. 2008) and the maintenance of biodiversity (Nichols et al. 2009) are more completely understood and able to be supported.

Studies on dung beetle taxonomy and ecology have been done across the globe by using direct observations, baited pitfall traps, natural dung pads and standardised dung pads (Fabre 1925; Landin 1961; Peck and Howden 1984; Lumaret and Kadiri 1995; Finn and Giller, 2000; Andresen 2001; Krell et al. 2003; Anlas et al. 2011a). Standardised dung pads formed from fresh, bulked, homogenized dung have been used to investigate various aspects of aggregation, coexistence, interscale movement, multifunctionality, and temporal and spatial resource partitioning. Species richness, abundance and biomass in dung are commonly used in statistical analyses to quantify and interpret the effects of variables that include soil type, vegetation type, diel activity, time of dung deposition, exposure period, grazing regime, season and pesticide use (Lumaret 1995; Krell et al. 2003, Hutton and Giller 2004, Krell-Westerwalbesloh et al. 2004, Horgan 2006, Jay-Robert et al. 2008, Beynon et al. 2012, Tixier et al. 2015; Verdu et al. 2015; Manning et al. 2017).

Various aspects of temporal changes in assemblages of dung beetle species have been investigated in temperate, Mediterranean and tropical environments (Lumaret and Kirk 1987; Caveney et al. 1995; Palestrini et al 1995; Finn et al. 1999; Krell et al. 2003; Krell-Westerwalbesloh et al. 2004; Horgan 2006; Jay-Robert et al. 2008; Nervo et al. 2017). The objective of the present study was to investigate temporal effects on the composition of dung beetle assemblages in the Kizilirmak Delta, a substantial part of which is a RAMSAR-listed conservation zone that has been proposed for World Heritage listing; its visitor centre is located approximately 40 km NW of the city of Samsun on the central Black Sea coast of Turkey (Plate 1). The study area, which has a mild climate with moderate seasonality (Köppen-Geiger classification: Csa) (Anon., 2017a), experiences a milder version of the Mediterranean climate that includes more

summer rain, and as a consequence, there is considerable dung beetle activity during the summer period.

Of the total Kizilirmak Delta area, 21,700 ha are wetland ecosystems; 11,580 ha of these habitats are composed of open water surfaces, freshwater and saltwater marshes, wet meadows and pastures. There are also 2,330 ha of sand and coastal dunes. The average height of the sand dunes, which are in a 200-300 metre wide band along the coast, is approximately 7 metres (Anon., 2017b). The dunal area, wet meadows and pastures are unfenced and grazed by free ranging cattle, horses, sheep and water buffaloes that collectively provide a year round supply of dung for coprophilous fauna and associated fauna.

Plate 1 Location of the study area: Kizilirmak Delta, Samsun Province, Turkey

Dung ball rollers tend to be better competitors for the dung resource than tunnellers, and tunnellers better competitors than dung dwellers (Doube 1990; also see section 1.4.6). What mechanisms allow tunnelling and dwelling species to persist in the face of potentially substantial competitive pressure from ball rolling species? Doube (1991)

reported that successional processes, diel activity and seasonality contribute to temporal resource partitioning among species. Lumaret (1995) reported that under Mediterranean climatic conditions, the majority of individuals exploit dung during the first two days of exposure, due to its rapid desiccation and the formation of a crust that limits its attractiveness.

In the body of research presented in this thesis, manipulations of standardised dung pads, namely the time of placement in the field, exposure period and size of pad, were expected to yield useful data on the behaviour of dung beetle species and genera, and their collective behaviour at the guild level, during community succession. The overarching hypothesis that was tested was: 'The three guilds in the dung beetle assemblage at the Kizilirmak Delta in Turkey are temporally separated in their use of dung'. In total, a series of five field experiments, including two unpublished experiments that involved the use of exclusion mesh, was conducted. The experiments were designed to principally but not exclusively focus on events within the first 24 hours after pad deposition because very limited information has been gathered in any environment for that critical period of colonisation and succession.

1.2 Aims and objectives

1.2.1 Conduct a survey of dung fauna in the Kizilirmak Delta in northern coastal Turkey

1.2.1.1 Determine the species richness and abundance of dung beetles at two adjacent sites on different soil types over a one year period

1.2.2 Investigate ball production by *Scarabaeus sacer* L., the large dung ball roller collected in 1.2.1.1

1.2.2.1 Deposit standardised dung pads of various sizes in the field to examine the effects of pad size on the number and size of balls produced and the temporal pattern of ball production by *S. sacer*

1.2.3 Investigate whether temporal resource partitioning is occurring among dung beetles by using standardised dung pads in a field experiment

1.2.3.1 Investigate temporal changes in dung beetle species and guild richness, abundance and biomass in standardised dung pads in early summer with two dung deposition times and seven dung collection times

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1.2.3.2 Investigate patterns in interspecific and interguild relationships through correlation analysis

1.2.4 Repeat the steps in 1.2.3 in late summer with six dung deposition times and three dung collection times

1.2.5 Exclude the dominant competitor *S. sacer* with mesh to determine the effects on community succession

1.2.5.1 Investigate temporal changes in dung beetle species and guild richness, abundance and biomass in standardised dung pads with meshed and non-meshed pads

1.2.6 Exclude increasing numbers of species from standardised dung pads with smaller and smaller mesh sizes to determine the effects on community succession

1.2.6.1 Investigate temporal changes in dung beetle species and guild richness, abundance and biomass in standardised dung pads with six different mesh sizes

1.3 Structure of thesis

1.3.1 Overview

This thesis consists of six chapters: an introduction; four core chapters that address the aims and objectives of the study in the form of published material; and a compilation of unpublished material, a synthesis and conclusions. The core chapters were written as a series of four related papers, all of which have been published in different, peer reviewed, international journals.

1.3.2 Chapter summaries

1.3.2.1 Chapter 1

Background to the study, aims and objectives, literature review and significance of the study.

1.3.2.2 Chapter 2

Dung beetles (Coleoptera: Scarabaeidae) utilizing water buffalo dung on the Black Sea coast of Turkey

This chapter reports on dung beetle diversity in a seasonal study on two adjacent soil types in the Kizilirmak Delta in Turkey. Species from three functional groups or guilds with different competitive abilities were collected. The species richness and abundance in the study area were deemed sufficient to conduct experiments on temporal separation of the guilds.

1.3.2.3 Chapter 3

Does one size suit all? Dung pad size and ball production by *Scarabaeus sacer* L. (Coleoptera: Scarabaeidae: Scarabaeinae)

This chapter reports on various aspects of dung ball production by the large ball roller *S. sacer*. The experimental protocol used in subsequent experiments (Chapters 4 and 5) was based on the methodology developed at this stage.

1.3.2.4 Chapter 4

How guilds build success; resource partitioning in a warm, temperate climate assemblage of dung beetles (Coleoptera: Scarabaeidae)

In the early summer of 2014, standardised dung pads were used to examine whether temporal separation, and by inference temporal resource partitioning, was occurring between two dung beetle guilds or functional groups, the dung dwellers and tunnellers. The parameters measured and compared were species richness, abundance and biomass. The experiment also investigated community succession and its relationship with temporal resource partitioning. To achieve that end, the network of interspecific, intraguild and interguild relationships underlying both succession and resource partitioning was determined through correlation analysis. The roles, or potential roles, of diel activity, habitat filtering, hierarchy of the competitive abilities of guilds, intraspecific and interspecific association, phylogenetic proximity, size difference, biomass, core species, facilitation and temporal niche partitioning on co-occurrence, are also discussed.

1.3.2.5 Chapter 5

Temporal resource partitioning and interspecific correlations in a warm, temperate climate assemblage of dung beetles (Coleoptera: Scarabaeidae)

The relationship between short term succession, temporal resource partitioning and interspecific and interguild relationships was explored in a dung beetle community through the use of standardised dung pads in the late summer of 2015. In addition, patterns in temporal resource partitioning and interspecific correlations across years and time of year were compared.

1.3.2.6 Chapter 6

Unpublished material, synthesis and conclusions

This chapter introduces unpublished material and synthesizes the findings of the previous four chapters, then discusses their implications for dung beetle ecology and ecological theory generally, describes limitations of the research, and identifies research possibilities.

1.4 Literature review

1.4.1 Introduction

The literature review backgrounds the rationale for this study which is stated in 'Significance of the study' (Section 1.5).

1.4.2 Evolution and taxonomy

There is conjecture as to whether ancestral dung beetles adaptively radiated in response to large quantities of reptile dung during the late Cretaceous Period (70-80 million years ago), as proposed by Chin and Gill (1996) and Krell (2006), or in parallel with the rapidly evolving mammalian diversity of the Tertiary Period (within the last 65 million years) (Halffter and Matthews 1966; Cambefort 1991a; Scholtz and Chown 1995, Scholtz 2009a). During the Tertiary Period, the increasing volumes of mammalian herbivore dung, with its highly nutritious liquid portion, generated numerous niche opportunities for the evolution of users which has resulted in more than 6,000 extant species of dung beetles, including approximately 5,000 species of

mostly tropical Scarabaeinae, and 150 species of Geotrupidae and 1,000 species of Aphodiinae, mostly in cooler regions, although many Aphodiinae species coexist with the Scarabaeinae in tropical areas (Scholtz 2009b). Across the globe, the Afrotropical region is by far the richest in species, with 2,000 species of Scarabaeinae (Davis and Scholtz 2001).

1.4.3 Distribution

Dung beetles have been reported from almost all environments, except Antarctica and Greenland (Cambefort 1991a). They occur across tropical (Kingston 1977; Peck and Howden 1984; Krell et al. 2003), subtropical (Bornemissza 1976; Doube 1990; Monteith and Storey 2013), warm temperate/Mediterranean (Davis 1987, 1993; Lumaret and Kirk 1987, 1991; Jay-Robert et al. 2008; Anlas et al. 2011a,b; Errouissi et al. 2011), cool temperate (Koskela and Hanski 1977; Davis 1993; Hutton and Giller 2004) and alpine (Lumaret and Stiernet 1991) environments that include grazing landscapes (Lumaret and Kirk 1987; Whipple 2011), savannahs (Kunz and Krell 2011), deserts (Matthews 1972; Halffter et al. 2011) and rainforests (Andresen 1999; Horgan 2006).

Approximately 700 Scarabaeidae species have been reported from Turkey, with 350 of them from the Laparosticti (mainly dung feeding species) (Carpaneto et al. 2000; Löbl and Smetana 2006). Most dung beetles studies in Turkey have been taxonomic (Balthasar 1952, 1963; Durand 1970; Tuatay et al. 1970, 1972; Pehlivan 1988, 1989, 1992; Baraud 1992; Lodos et al. 1999; Carpaneto et al. 2000; Tauzin 2000, 2001, 2002; Dellacasa and Kirgiz 2002; Lobl and Smetana 2006; Bellmann 2007; Rozner and Rozner 2009; Senyuz et al. 2013; Ziani and Sama 2013). Other studies (Senyüz 2004; Senyuz and Sahin 2009; Anlas et al. 2011a,b; Sullivan et al. 2016a,b; Sullivan et al. 2017a,b) have had an ecological focus.

1.4.4 Ecology of animal dung

Ephemeral resource patches include animal dung pads, leaf packs in streams, fruits, mushrooms and carrion (Finn 2001). Dung pads are scattered microhabitats of high quality resources of relatively small size and short duration that support complex communities (Mohr 1943) with representatives from 26 families of Diptera, Coleoptera and Hymenoptera (Hanski 1991a), and other groups, including annelids and mites

(see section 1.1). Heterotrophic succession occurs in dung pads as they age and amongst the earliest colonisers are the dung beetles of the families Scarabaeidae and Geotrupidae (Valiela 1974; Koskela and Hanski 1977; Hanski 1987; Davis 1993; Barth et al. 1994; Lumaret and Kadiri, 1995; Jay-Robert et al. 2008; Tixier et al. 2015; Sullivan et al. 2017a,b). Dung pads are consumed and used for oviposition by dung beetles and other insects, including flies (Hanski 1991a). Some dung beetle species prefer fresh pads, others prefer older pads and the age of the pad appears to make little difference to some species (Doube 1991). The body size range, life histories and feeding behaviour of dung beetle larvae and adults have been documented and discussed in considerable detail (Cambefort 1991b; Doube 1991; Holter 2016).

1.4.5 Factors influencing local community

Local dung beetle communities reflect the combined effects of many abiotic and biotic factors that include soil and vegetation type (Doube 1983; Kirk 1983; Lumaret and Kirk 1987; Krell et al. 2003; Sullivan 2016a), source of dung (herbivore, carnivore and omnivore) (Bernon 1981; Doube 1987; 1991; Dormont et al. 2007; Filgueiras et al. 2009; Whipple 2011), age of dung pad/dung moisture level (Doube 1987; Barth et al. 1994; Kryger et al. 2006), size of pad (Peck and Howden 1984; Finn and Giller 2000), segment of pad (Barth 1994; Lumaret 1995), soil moisture/rainfall events (Kingston 1977; Lumaret 1978), altitude (Mittal 1981; Moron and Zaragoza 1976; Avila and Pascual 1987), latitude (Kirk and Ridsdill-Smith 1986; Hanski 1991b), mean temperature/season (Lumaret 1979; Davis 1989) and diel activity (Bernon 1981; Hernandez 2002; Krell et al. 2003; Sullivan et al. 2016b, 2017). Of these, latitude, climate, altitude and soil and vegetation types typically shape regional communities; Doube (1991) reported that dung beetle communities in southern Africa are determined primarily by soil type, and to a lesser degree, by vegetation and dung types.

1.4.6 Functional groups

Most dung beetles use one of three broad nesting strategies: paracoprid (tunnelling) species dig burrows and construct nesting chambers, usually below the dung pad; most telecoprid (ball rolling) species form and roll balls some distance before burial; and endocoprid (dung dwelling) species live in or brood their offspring inside the dung

mass itself or at the dung/soil interface (Halffter and Matthews 1966; Bornemissza 1969; Hammond 1976; Rougon and Rougon 1980; Walter 1980; Halffter and Edmonds 1982; Klemperer 1983). The fourth group, the kleptoparasites, steal dung from or deposit their eggs in the broods of paracoprid or telecoprid species (Cambefort 1991c). Brussaard (1987) and Doube (1990) used the term 'kleptocoprid' to describe the same group. Doube (1990) developed a classification system for the analysis of the structure of dung beetle assemblages by dividing them into seven functional groups, with a clear hierarchy among the groups in terms of their ability to compete for dung.

1.4.7 Ecological functions and ecosystem services

Maintaining the connectivity of ecological functions ("multifunctionality") is critical to the sustainability of ecosystems (Nervo et al. 2017). Dung beetles provide a suite of ecological functions and ecosystem services (Slade et al. 2007; Nichols et al. 2008; Beynon et al. 2012; Chamberlain et al 2015; Tixier et al. 2015). They use dung as a food and nesting resource and consequently provide essential services that include degradation of dung, including aeration of the soil and organic matter incorporation; secondary seed dispersal; and suppression of vertebrate parasites and pest fly control (Bryan 1976; Wallace and Tyndale-Biscoe 1983; Mathison and Ditrich 1999; Waterhouse and Sands 2001; Andresen and Feer 2005; Bang et al. 2005; Horgan 2005). Furthermore, dung beetles influence at least seven ecological functions by facilitating dung removal, transportation of dung-derived nitrogen (DDN) into the soil, microbial ammonification and nitrification processes, the uptake of DDN by plants, herbage growth and botanical composition (Nervo et al. 2017).

Many species of scarabaeine dung beetles have been deliberately introduced into foreign environments to provide the biological control of flies and other ecosystem services in pastoral landscapes where native dung beetle species have not coped with the enormous amounts of dung produced by large, introduced herbivores, especially cattle, including Australia (Bornemissza 1976), New Zealand (Blank et al. 1983), the USA (Fincher 1986) and South America (Barbero and Lopez-Guerrero 1992).

1.4.8 Sampling methods

The detailed investigation of community succession in natural dung pads is inherently difficult, given the randomness of their time of deposition and spatial arrangement

(Barth et al. 1994). Particularly in the last 30 years, numerous ecological studies have investigated dung beetle community composition with other methods, especially with baited pitfall traps (Peck and Howden 1984; Davis 1996; Larsen and Forsyth 2005), and also through the deployment of standardised dung pads (Barth et al. 1994; Lumaret and Kadiri 1995; Krell et al. 2003; Jay-Robert et al. 2008; Sullivan et al. 2017a,b), but the use of natural dung pads continues (Hutton and Giller 2004; Anlas et al. 2011b; Sullivan et al. 2016a). Pitfall trapping is useful for sampling the 'presence/absence' of species in a locality, as well as seasonal activity, and can also be used to investigate the attractiveness of dung of different types and ages, whereas the use of standardised pads allows experimental studies of community composition and the activity of actual assemblages, thus both approaches have utility (P. Giller, pers. comm.).

Baited pitfall traps captured a much larger number of individuals than the same amount of dung exposed on the soil surface (Lobo et al. 1988). However, there was no significant difference between the numbers of 14 of 17 species of large, crepuscular/nocturnal, tunnelling species recovered from pitfall traps and standardised pads (Doube and Giller 1990). These conflicting results cast some doubt on the ability of catches in pitfall traps to accurately represent the composition of dung beetle communities in natural pads. In contrast, Barth et al. (1994) reported that the total numbers of coleopteran families and species and abundance of beetles recovered from natural and standardised pads were almost identical.

The number of beetles collected from standardised pads at a particular time is the net result of immigration and emigration (Doube and Giller 1990) which implies that standardised pads contain actual communities at any particular point in time. The protocol for ecological assemblage studies should include the use of standard sized dung pads placed directly on the ground to simulate natural conditions, which enables the collection of only the actual users of the resource by allowing temporary visitors to leave (Krell 2007). However, Krell et al. (2003) acknowledged that the use of standardised pads underestimates the number of ball rollers but argued that their use is preferable to pitfall trapping in which overestimated groups are not distinguishable.

1.4.9 Conservation and management issues

Most dung beetle species face multiple conservation threats, including habitat destruction or degradation and the hunting of large mammals (Lobo 2001; Nichols et al. 2009), abandonment of traditional grazing areas (Jay- Robert et al. 2008; Macagno and Palestrini 2009) and the parasiticides used to control endo- and ectoparasites of dung producers, mostly herbivores (Ridsdill-Smith1988; Cruz Rosales et al. 2012). Climate change, and to a lesser extent their commercial trade, also threaten dung beetle diversity. Nichols and Gardner (2011) reported that more than 12% of all dung beetle species are threatened with extinction.

1.5 Significance of the study

A better understanding of the interactions of dung beetle species at the interspecific and guild levels has global ramifications because of the numerous ecological functions and ecosystem services they provide. The taxonomy and ecology of dung beetles has been relatively well studied worldwide; see Chapter 2 (Section 2.5) for the numerous taxonomic studies done in Turkey. However, there is a paucity of information on their ecology in Turkey, with only a small number of seasonal studies of species richness and abundance having been done (Senyüz 2004; Senyuz and Sahin 2009; Anlas et al. 2011a,b). Before the present study, there had been no research into the dung fauna at the Kizilirmak Delta. Ball rolling, dung dwelling and tunnelling guilds of dung beetles co-occur there (see Appendix 1 and Plate 9). Multispecies, native assemblages with three guilds on such grazing sites with little or no insecticide use are conducive to informative ecological studies. The sand dune site was chosen for the series of experiments because it is the only area of the delta where the iconic ball rolling species, *Scarabaeus sacer* L., is found.

Dung fauna, including dung beetles, often arrive within seconds of the deposition of a dung pad and the processes of succession and temporal separation and resource partitioning commence at that time. There have been studies of colonization and relatively short term succession in dung beetle assemblages in tropical environments where ball rollers and large tunnellers tend to dominate assemblages (Walter 1980; Montes de Oca and Halffter 1995; Krell-Westerwalbesloh et al. 2004). However, very short term temporal changes in the species richness, abundance and biomass of dung beetles have not been comprehensively investigated in any environment.

The presence of only one large species, the ball roller, *S. sacer*, which is a dominant competitor, allowed an experimental focus on its behaviour during ball production. In addition, assuming that the majority of the dwelling species have established breeding populations in the area, what mechanisms underpin their persistence in the face of potential competition from *S. sacer*, and tunnelling species? Are diel separation, temporal separation and temporal resource partitioning involved?

These questions were addressed through the manipulation of the time of deposition and the exposure period of standardised dung pads to determine whether they affect the mean abundance of the dwelling and tunnelling species, with a particular emphasis on the first 24 h. Correlation analysis was used to complement those results by determining the strength of the network of interspecific relationships occurring during community succession.

Overall, this study was directed to achieving a better understanding of the interaction of dung beetles at the species and guild level and therefore potentially of considerable value due to the ecological functions and ecosystem services dung beetles provide worldwide. It was also anticipated that the methodology and results would be relevant to the study of the co-occurrence of other dung fauna and fauna in other ephemeral resource patches.

CHAPTER 2   Dung beetles (Coleoptera: Scarabaeidae) utilizing water buffalo dung on the Black Sea coast of Turkey

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2.1 Abstract

There have been few ecological studies of dung beetles (Coleoptera: Scarabaeidae) from the Black Sea Region of Turkey. In the RAMSAR-listed wetland system of the Kizilirmak Delta of Turkey's central Black Sea coast, seasonal grazing by domesticated water buffalo produces plentiful dung from April to November. Twenty-three species of dung beetles from 13 genera of Aphodiinae and 4 genera of Scarabaeinae were collected from their dung on two adjacent soil types in 2013. The species were from three functional groups, namely dung dwelling (12), tunnelling (10), and ball rolling (1). Thirteen and fourteen species were collected in spring/summer and autumn, respectively, with only 4 species in common. There was a distinct shift from Scarabaeinae (8 of 13 species) in spring/summer to Aphodiinae (10 of 14 species) in autumn. The ten species collected on sandy clay loam soil were a subset of the 23 species on the sand dunes. On the sandy clay loam, high water tables in winter and soil cracking in summer may exclude deeper tunnelling species. The 3:1 ratio of dung dwelling species on the sand compared to the sandy clay loam may suggest a more appropriate dung moisture regime over time that favors successful breeding on the sand.

Key words: Kizilirmak Delta, insects, community, coprophilous, interspecies competition, season

2.2 Introduction

The alluvial plains and associated coastal dune systems of the Kizilirmak Delta in Samsun Province of Turkey have a long history of free-range grazing by water buffalo (*Bubalus bubalis* L.), cattle (*Bos primigenius taurus* L.), sheep (*Ovis aries* L.), and wild horses (*Equus ferus caballus* L.), which collectively produce large volumes of dung all year round, particularly in spring and summer. Grazing, especially by the hundreds of water buffalo, plays a major role in structuring the vegetation in the Kizilirmak Delta, including its permanent and ephemeral wetlands and adjacent coastal sand dune systems. The buffaloes spend a considerable amount of time grazing on aquatic plants, which later provides a large additional amount of dung in the adjoining landscape.

Finn (2001) reported dung, leaf packs in streams, fruits, mushrooms, and carrion as ephemeral resource patches. More specifically, Mohr (1943) described dung pads as scattered microhabitats of high-quality resources of relatively small size and short duration that support complex communities. Factors that collectively influence the composition of dung beetle communities include soil and vegetation type (Lumaret and Kirk 1987; Krell et al. 2003), source of dung (herbivore, carnivore, and omnivore) (Dormont et al. 2007; Filgueiras et al. 2009; Whipple 2011), age of dung (Barth et al. 1994; Kryger et al. 2006), size of pad (Peck and Howden 1984; Finn and Giller 2000), soil moisture/rainfall events (Kingston 1977; Lumaret 1978), altitude (Mittal 1981; Avila and Pascual 1987), latitude (Kirk and Ridsdill-Smith 1986; Hanski 1991a), mean temperature/season (Lumaret 1979; Davis 1989), and diel activity (Hernandez 2002; Krell et al. 2003).

Intense competition at the dung pad has triggered niche splitting and speciation (Halffter and Edmonds 1982). Most dung beetles use one of three broad nesting strategies: paracoprid (tunnelling) species dig burrows and construct nesting chambers, usually below the dung pad; telecoprid (ball rolling) species form and transport balls some distance before burial; and endocoprid (dwelling) species live in and brood their offspring inside the dung mass itself or at the dung/soil interface (Halffter and Matthews 1966; Hammond 1976; Rougon and Rougon 1980; Halffter and Edmond 1982; Klemperer 1983). The fourth group is the kleptoparasites, which steal dung from or deposit their eggs in the broods of paracoprid or telecoprid species (Hammond 1976). Brussaard (1987) and Doube (1990) used the term 'kleptocoprid' to describe the same group.

Approximately 350 species of Laparosticti, which are mainly dung feeding Scarabaeidae, have been reported from Turkey (Carpaneto et al. 2000; Löbl and Smetana 2006). However, there have been few dung beetle studies from the Black Sea region (Lodos et al. 1999; Şenyüz et al. 2013). The current study reports the results of a seasonal survey of the dung beetle species on two soil types in the Kizilirmak Delta on the central Black Sea coast of Turkey and discusses aspects of the ecology of the species collected.

2.3 Materials and methods

The climate of coastal areas of Samsun Province in Turkey is moderated by close proximity to the Black Sea and is characterized by relatively dry, warm/hot summers and cool, wet winters. In the late spring (May), early summer (June), and autumn (October, November) of 2013, dung beetles were collected from natural water buffalo dung pads on two soil types in the Kizilirmak Delta wetlands complex; the water buffalo are removed by their owners from November to April and thus no collections were done. Details of the physical and chemical characteristics of the two soil types are provided in Table 2.1.

During the study, samples were collected every 2 weeks from ten dung pads of various ages, shapes, and sizes on each soil type at various times of the day and night. Using a method modified from Krell (2007), each dung pad was sampled by collecting approximately 700 g and placing it in a 10 L bucket. The soil directly below and close to 15% of all pads was excavated to 10 cm to collect tunnelling species that may not have been collected in pads or at the pad/soil interface. Deeper tunnels were excavated to full depth. The excavated soil was added to the dung sample. Samples were flooded with water and agitated with a wooden paddle to disperse dung material. Beetles that floated to the surface were removed with a fine mesh sieve and collected with flexible forceps or a fine brush, or collected directly from the water surface. The agitation process was continued until no more beetles appeared. The residual material was then sifted to collect any remaining specimens. Separately, a small number of older, drier pads were also sampled by fracturing them into small pieces over a plastic sheet. Additionally, dung beetles were collected from both soil types in CSR-type pitfall traps (5/site) baited with 700 g of fresh water buffalo dung and using ethylene glycol as the preservative, as per the method of Lobo et al. (1988), although their use was quickly discontinued because of the by-catch of non-target species. Ball rolling dung beetles were also hand-collected from dung pads. As per the method of Floate and Kadiri (2013), specimens were stored in 70% ethanol in labelled containers before identification.

All the species collected were identified by the third author (JPL), using the keys of Baraud (1985, 1992). Because the closely related species *Onthophagus medius* (Kugelann) has been reported from Turkey (Rossner et al. 2010; Anlas et al. 2011a), the identification of *Onthophagus vacca* (L.) specimens was confirmed with standard molecular tools, using two genetic markers, CO1 and ITS2.

2.3.1 Statistical analysis

The Sørensen similarity index (S_S) (Krebs, 1998; Balmer, 2002) was used to compare the dung beetle species diversity from the two soil types in the current study. Sørensen's formula, which is applied to presence/absence data, is:

$$S_S = \frac{2a}{(2a + b + c)},$$

where 'a' is the number of shared species, 'b' is the number of species only in collection 1, and 'c' is the number of species only in collection 2.

2.4 Results

Twenty-three species from 17 genera belonging to 2 subfamilies, Aphodiinae and Scarabaeinae, were identified from the 2,594 specimens collected. Species were distributed among the three major guilds, namely dung dwellers (12 species), tunnellers (10 species), and rollers (1 species) (Table 2.2). No kleptocoprids were collected. Across the two soil types, *Colobopterus erraticus* (L.) and *Onthophagus taurus* (Schreber) were the most common tunnelling species, and *Melinopterus consputus* (Creutzer) and *Acanthobodilus immundus* (Creutzer) were the most common dwellers. All the Scarabaeinae species, except *Scarabaeus sacer* L., and *C. erraticus* from Aphodiinae, are tunnellers. All the other Aphodiinae are dwellers, and the one Scarabaeini species, *S. sacer*, is a roller.

All 23 species were collected on the sand and a subset of 10 species (6 tunnellers and 4 dwellers) was collected on the sandy clay loam. For the seasonal comparisons of species richness, all samples were aggregated for each season's data. In the spring/summer, there were 8 tunnellers, 4 dwellers, and 1 roller on the sand and 6 tunnellers and 2 dwellers on the sandy clay loam. In the autumn, an additional 8 dwellers and 2 tunnellers, and 2 dwellers, were collected on the sand and the sandy clay loam,

respectively. Fourteen species were collected in autumn and 13 species in spring/summer, with 4 species present at both times (Table 2.2).

There was a distinct shift from Scarabaeinae (8 of 13 species) in spring/summer to Aphodiinae (10 of 14 species) in autumn. In other words, in autumn, the number of Scarabaeinae species fell from 8 to 4 and the number of Aphodiinae species rose from 5 to 10. Additionally, only 2 of 13 species of Aphodiinae and 2 of 10 species of Scarabaeinae were collected in both autumn and spring/summer (Table 2). For the two soil types,

$$S_S = \frac{2x10}{(2x10+13+0)} = 0.61,$$

where the number of species on both sand and sandy clay loam was 10, the number of species only on the sand was 13, and the number of species only on the sandy clay loam was 0.

2.5 Discussion

All 23 species reported in the present study (Table 2.2) have been reported previously from Turkey (Balthasar 1952, 1963; Durand 1970; Tuatay et al. 1970, 1972; Pehlivan 1988, 1989, 1992; Baraud 1992; Lodos et al. 1999; Carpaneto et al. 2000; Tauzin 2000, 2001, 2002; Dellacasa and Kirgiz 2002; Şenyüz 2004; Löbl and Smetana 2006; Bellmann 2007; Rozner and Rozner 2009; Şenyüz and Şahin 2009; Anlas et al. 2011a,b; Şenyüz et al. 2013; Ziani and Sama 2013). Lodos et al. (1999) reported 36 species from a general survey of the western Black Sea region of Turkey, with only 10 Aphodiinae species in common with the present study. Anlas et al. (2011a) reported 33 species from cow dung in a 2-year study in Manisa Province in south-western Anatolia of Turkey, with 12 species in common with the present study. The species counts from the present study and that of Anlas et al. (2011a), which are from very different grazing environments in Turkey, are much higher than from pastures in Hawaii (Harris et al. 1982), South Africa (Davis 1987), Australia (Edwards 2003), Mexico (Anduaga 2004) and Canada (Kadiri et al. 2014), where there are normally less than 10 species. In addition, Galante et al. (1991) reported 18 species (only rollers and tunnellers) from Spain, and Lumaret et al. (1992) reported 43 species from France.

Furthermore, the current study reports 13 species of Aphodiinae (57% of all species), compared to the 8 species (24% of all species) reported by Anlas et al. (2011a). Rowjewski (1983) reported that *C. erraticus* is a tunneller, which makes it the only non-endocoprid Aphodiinae species in the current study. Additionally, species from the same three functional groups as in the current study were reported from Turkey by Lodos et al. (1999) and Anlas et al. (2011a).

In the present study, there was a 2.3:1 ratio of dung beetle species on the pure sand (23 species) compared to the sandy clay loam (10 species), which is a substantial disproportionality. The greater ease of tunnelling in the sand and/or the risks attached to tunnelling in the silty loam (Lumaret and Kirk 1987) is indicated by the almost 2:1 ratio of tunnellers plus rollers on the sand dunes (11 species) compared to the sandy clay loam site (6 species). Lumaret and Kirk (1995) reported that for numerous species that nest in the soil, the capacity of the soil to retain water, the depth of the saturated horizon, and also the duration of saturation, determine the success or failure of nesting. The relatively depauperate tunnelling dung beetle fauna on the sandy loam site in the present study probably reflects its seasonal inundation and high water table, especially in winter and spring, which create adverse conditions for adults, eggs, larvae and pupae alike.

Additionally, there were 12 and 4 dung dwelling species collected on the sand dunes and sandy clay loam, respectively. It appears that high sand substrates are more favorable for dwelling species; after the dung pad is deposited on the sand surface, some of the excess moisture is absorbed into the macropores in the sand immediately beneath the pad, which dries the dung and allows it to quickly reach the appropriate moisture content for oviposition by Aphodiinae (Lumaret, 1975). Thereafter, the dung pad gradually reabsorbs moisture from the damp sand under the dung, which helps keeps the inside of the dung moist for a relatively longer period. The interior of the dung pad also retains moisture by the rapid formation of a crust on the surface that quickly becomes almost impermeable, hence limiting the evaporation of moisture. Thus, water is trapped inside the dung for long enough for larvae to reach the pupal stage. On clay soils, the water present in dung immediately after its deposition (ruminant dung contains approximately 80% water initially) is less easily lost to the underlying soil. Paradoxically, especially in summer, the dung dries faster because moisture gradually moves by capillary action into the micropores of the clay particles and cannot be reabsorbed by the pad later, making such substrates less favorable for the breeding of Aphodiinae (Lumaret and Kirk 1987).

Lumaret and Kirk (1991) stated that Mediterranean dung beetles are most active before and after the summer drought, with the major peak of activity occurring at the end of spring (May and June) and a smaller peak in autumn. Haloti et al. (2006) also reported that some species are active in late autumn and winter. Even though the summer drought is generally less pronounced in the current study area in the Black Sea region than in the Mediterranean region, late spring/early summer and autumn surveys were conducted in anticipation of those same peaks. The majority of sampling was undertaken in May and June when mean daily temperatures were increasing and after several substantial rainfall events. The rest of the sampling (40% of all pads) was conducted in autumn (October and November). This was done on the expectation of a second increase in dung beetle activity driven by rain periods (Lumaret and Kirk 1991). This strategy proved fruitful as a greater number of species was collected in autumn (14) than spring/summer (13). The phenomenon of higher diversity of Scarabaeinae and Aphodiinae species in summer and autumn, respectively, was also reported by Lumaret and Kirk (1991) and Errouissi et al. (2011). In conclusion, the current research provides further confirmation that soil type and season influence the composition of local dung beetle assemblages.

2.6 Acknowledgements

Table 2.1 Chemical and physical characteristics of the locations from which dung beetles were collected in the Kizilirmak Delta in Samsun Province, Turkey

Locations	Coordinates	Depth (cm)	Clay (%)	Silt (%)	Sand (%)	Texture	pH (1:1)	EC (dS/m)	OM (%)
Sand dune site	41°39′26″N 36°04′03″E	0–20	0	0	100	S	8.05	0.03	1.42
		20–40	0	0	100	S	8.51	0.04	1.25
Sandy loam site	41°40′16″N 36°02′29″E	0–20	18.4	7.2	74.4	SCL	8.36	1.26	4.94
		20–40	18.9	11.3	69.4	SL	8.86	0.29	2.45
		40–60	22.7	6.5	70.8	SL	8.58	0.66	2.18

S: Sand; SCL: Sandy clay loam; SL: Sandy loam; pH: Soil reaction (1:1, w:v); EC: Electrical conductivity; OM: Organic matter

Table 2.2 Dung beetle species collected from water buffalo (*Bubalus bubalis* L.) dung pads, dung-baited pitfall traps and from the ground in the Kizilirmak Delta of Samsun Province, Turkey

Subfamily	Species	Season		Location	
		Spring /summer	Autumn	I	II
				Sand	Sandy clay loam
Aphodiinae	*Acanthobodilus immundus* (Creutzer)*	+	+	+	+
	Aphodius fimetarius (L.)*	-	+	+	-
	Bodiloides ictericus subsp. *ghardimaouensis* Balthasar*	-	+	+	-
	Bodilus lugens (Creutzer)*	-	+	+	-
	Chilothorax distinctus (Muller)*	-	+	+	-
	Colobopterus erraticus (L.)**	+	-	+	+
	Labarrus lividus (Olivier)*	+	-	+	-
	Melinopterus consputus (Creutzer)*	-	+	+	+
	Nialus varians (Duftschmidt)*	-	+	+	-
	Nimbus contaminatus (Herbst)*	-	+	+	-
	Otophorus haemorrhoidalis (L.)*	-	+	+	+
	Phalacronothus quadrimaculatus (L.)*	+	-	+	+
	Subrinus sturmi (Harold)*	+	+	+	-
Scarabaeinae	*Caccobius schreberi* (L.)**	+	-	+	+
	Euoniticellus fulvus (Goeze)**	+	-	+	+
	Euoniticellus pallipes (Fabricius)**	+	+	+	-
	Onthophagus furcatus (Fabricius)**	-	+	+	-
	Onthophagus nuchicornis (L.)**	+	-	+	-
	Onthophagus opacicollis Reitter**	-	+	+	-
	Onthophagus ruficapillus Brullé**	+	-	+	+
	Onthophagus taurus (Schreber)**	+	+	+	+
	Onthophagus vacca (L.)**	+	-	+	+
	Scarabaeus sacer L.***	+	-	+	-

*: dweller, **: tunneller, ***: roller; +: present, -: absent

Plate 2 Free ranging, domesticated water buffalo at the Kizilirmak Delta

Plate 3 View of the study site in the Kizilirmak Delta with standardised dung pads marked with pegs in replicated plots

Plate 4 Production of a standardised dung pad from homogenised water buffalo dung in a plastic mould

Plate 5 Placement of a standardised dung pad in an experiment in the Kizilirmak Delta

Plate 6 *Scarabaeus sacer* L., including male and female pairs, constructing balls from a standardised 500 g dung pad in the Kizilirmak Delta in Samsun Province, Turkey

Plate 7 Separation of dung beetles (Coleoptera: Scarabaeidae) from water buffalo dung by flotation in water
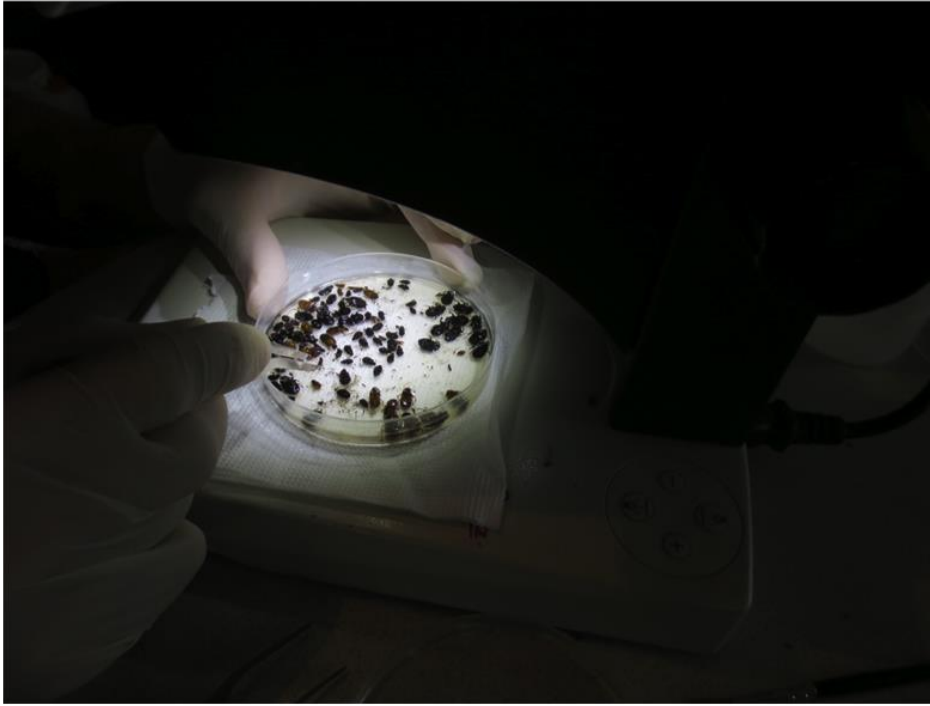
Plate 8 Separation of dung beetle species under microscope

Plate 9 Size range of dung beetle species collected in the Kizilirmak Delta in Turkey (left: ball roller; middle: four tunnelling species; right: dung dweller)

CHAPTER 3 Does one size suit all?; dung pad size and ball production by *Scarabaeus sacer* (Coleoptera: Scarabaeidae: Scarabaeinae)

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3.1 Abstract

Large, ball rolling dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are competitively dominant and can strongly influence community succession in dung pads. Ball production by *Scarabaeus sacer* L. was recorded in the Kizilirmak Delta on the Black Sea coast of Turkey by using standardised dung pads from 125 g to 2,000 g. Utilisation of pads across the 16-fold range of pad sizes demonstrated behavioural variation that may reduce intraspecies competition. Ball production was highly concentrated, with 66 (61%) produced from 8 pads of the 3 largest pad sizes, which may be related to chemical attraction between males and females. Ball size increased with increasing pad size ($P < 0.05$) but the number of balls produced per 100 g of dung decreased with increasing pad size ($P < 0.01$). Pad size for maximum ball production and ball size were 1,371 g and 1,260 g, respectively. The highest and lowest percentage of dung used for ball production was 43% of 125 g pads and 13% of 2,000 g pads, respectively. Ball production and time of day were significantly related ($P < 0.01$); *S. sacer* was almost exclusively nocturnal, with 59% of all balls produced between 21.00 and 22.00. This optimum period for ball production early in the night may be a compromise between reduced risk of predation and the increased energy costs of ball production as the temperature falls.

3.2 Introduction

Ball production and rolling in dung beetles probably evolved to expedite escape from intraspecific and interspecific competition at the dung pad (Halffter and Matthews 1966; Scholtz 2009), and is a characteristic behaviour of the Scarabaeini of Scarabaeidae (Cambefort 1991c). Hanski and Cambefort (1991a) ascribed the morphology of dung ball rollers (telecoprids) to a series of trade-offs between the ability to make and roll balls, and to burrow, and the size of the ball and the ease with which it can be rolled.

The size of the dung ball is related to the size of the individual producing it (Halffter and Matthews 1966) and food balls tend to be smaller than brood balls (Hanski and Cambefort 1991a). In a specific case, Edwards and Aschenborn (1988) reported that food balls rolled by individual males or females of *Kheper nigroaeneus* (Boheman) were smaller than brood balls rolled by individuals or pairs. Irrespective of the type of ball, some species make larger balls than others (Hanski and Cambefort, 1991a).

Ball weight and the ratio of ball weight to body weight vary greatly across species. For single beetles, fresh ball weight varied from 0.03 g in *Sisyphus seminulum* Gerstaecker [Cambefort (pers. obs.) in Hanski and Cambefort, 1991a] to 30 g in *Scarabaeus sacer* L. (Marsch 1982), and the ratio of ball weight to body weight ranged from 6:1 in *S. seminulum* to 36:1 in *Neosisyphus barbarossa* (Wiedemann) (Hanski and Cambefort, 1991a). Doube (1990) reported that large telecoprids produce balls weighing 5 to 20 times more than their body weight. Once the ball is formed, rollers try to maintain a straight rolling path away from the dung source (Matthews 1963; Byrne et al. 2003) by using various celestial cues such as the position of the sun, moon and stars (Halffter and Matthews 1966; Dacke et al. 2004, 2013) and environmental cues such as wind direction and slope (Matthews 1963).

Field research into the feeding behaviour of telecoprids using natural dung pads poses considerable difficulties, including deposition of pads by different species at different times; wide dispersion of pads in varying physical environments; and the different size, shape and composition of pads. These problems can be circumvented by the use of standardised pads because their source, size and shape can be predetermined. In a

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study that did not include rollers, Barth et al. (1994) reported few differences in the communities of insects colonizing natural and standardised pads. Krell et al. (2003) used standardised pads to investigate the ecology of dung beetle assemblages that included rollers.

The large dung ball rollers, including *S. sacer*, are dominant competitors because they rapidly remove dung for their exclusive use (Doube 1990, 1991), a behaviour that can strongly influence subsequent colonisation and succession events in dung beetle communities. If *S. sacer* were to use dung pads of different sizes to different extents, it would likely have direct and substantial effects on local community assemblages. However, we have not found evidence of replicated plot field studies on the effects of dung pad size on ball production and the amount of dung used.

Scarabaeus sacer has been reported from more than 30 countries in a discontinuous belt from the far west of southern Europe and northern Africa across central Asia to western China (Lobl and Smetana 2006). Marsch (1982) and Baraud (1992) reported *S. sacer* as nocturnal but it has also been recorded as crepuscular (Lumaret 1990; Verdú et al. 2004) and diurnal (Lumaret 1990; Martin-Piera and Lopez-Colon 2000; Verdú et al. 2004). These varying activity periods across different environments indicate a degree of behavioural variation. *Scarabaeus sacer* inhabits sandy environments where normally the scarcity of food strongly influences its feeding and mating behaviour (Halffter et al. 2011). The current study aimed to determine whether the number and size of balls produced by *S. sacer* increases with dung pad size, and also the daily pattern of dung ball production.

3.3 Materials and methods

Study site

The experiment was conducted along the exposed ridge line of a coastal sand dune (41º39´26´´ N, 36º04´03´´ E) adjacent to the Kizilirmak Delta on the central Black Sea coast of Turkey from 9 to 11 June, 2014. The sparse vegetation on the dune was dominated by *Euphorbia terracina* L. Free-ranging, domesticated water buffalo (*Bubalus bubalis* L.) regularly deposit dung pads on the dune system between a large freshwater lake and the sea, attracting large numbers of *S. sacer*, which was identified by the third author using the key of Baraud (1992).

Experimental procedure

A preliminary experiment had determined that newly deposited water buffalo dung is very moist (mean water content = 84% (n=4)) and generally avoided by *S. sacer*. If they did use it, they tended to scrape off portions of the drier crust and aggregate these scrapings into a ball. Therefore, for the current study, in the 1 h period immediately before establishment of the experiment, approximately 50 kg of dung was collected from 30 natural pads that ranged from very fresh to 24 h old. There were low levels of infestation by small tunnelling and dung dwelling species in some of these natural pads. Small dwelling and tunnelling dung beetles regularly occur in balls being rolled by *S. sacer* at the study site so it was assumed that their presence in experimental pads would not deter ball production.

The experiment employed a randomized complete block design with 5 different dung weights and 6 replicates to determine the effects of dung pad weight on ball production by *S. sacer* over a 48 h period. The fifty kilograms of dung was bulked and homogenized before being used to form standardised dung pads (Barth et al. 1994; Lumaret and Kadiri 1995; Krell 2007) in 5 circular, plastic moulds of the same shape but of different diameters and depths. The formed pads covered the 16-fold range of 125 g, 250 g, 500 g, 1000 g and 2000 g. The experiment was commenced at 18:00 on 09 June, 2014 when all 30 experimental pads were deployed, and terminated at 18:00 on 11 June, 2014. During the study, temperatures ranged from 13 ^{o}C to 25 ^{o}C in the shade at 1 m above the ground, with clear skies for the entire period and very similar conditions on both days. Sunrise and sunset on 09 June, 2014 were at approximately 5:05 and 20:10, respectively. Moonrise on 09 June and 10 June, 2014 were 16:03 and 17:08, respectively, and moonset on June 10 and 11 June, 2014 were 2:55 and 3:36, respectively. Meridian passing was at 21:32 pm (85.7% illumination) and 22:24 pm (92.7% illumination) on 09 June and 10 June, respectively. The full moon was on 13 June, 2014 (Anonymous 1995).

The six replicates were arranged in 2 parallel lines of 3 replicates, with 10 m between the lines, a 6 m gap between replicates and 5 m between pads. A pad of each of the 5 weights was randomly allocated to each of the 6 replicates. The total length of each row was 72 m. All natural pads suitable for use by *S. sacer* were removed from within the experimental area and from a surrounding 30 m belt at the beginning of the experiment to enhance the attractiveness of the experiment pads.

Counting rollers only at the time of peak activity underestimates their numbers (Krell et al. 2003), so the pads were kept under observation for the full duration of the experiment. The study coincided with an almost full moon which assisted the visibility of the observers who had unobstructed views of pads as they walked along the outside of the lines at 15 minute intervals, and at 5 to 10 minute intervals during peak ball production periods. The observers wore dark clothing and used low-powered torches to enhance visibility whilst minimizing potential disturbance of *S. sacer* individuals. Extreme care in the form of slow movements and hand-signalling was also exercised to minimize disturbance of *S. sacer.*

The number of balls produced each hour by *S. sacer* from each pad was recorded during the study, with a ball considered produced if it was clearly distinguishable from the dung pad. Additionally, on a small number of occasions, the curved excavations on the top and sides of pads that are indicative of ball production were used to infer that balls had been produced and rolled away unseen by observers.

Both the number of balls produced and number of balls produced per 100 g were compared for the 5 dung pad sizes. In addition, the dimensions of a sample of balls produced from all dung pad sizes was measured with calipers while *S. sacer* was 'resting' during ball rolling or during the early stages of burial. The balls longest and shortest dimensions were measured and because most balls were approximately spheroidal in shape, their volumes were determined with the equation $4/3.\pi.a^2.c$ (a = equatorial radius; c = polar radius), except in one case where the dimensions were equal and volume was determined as a sphere ($4/3.\pi.r^3$) (Anonymous 2008). The volume of dung removed from a particular pad size was determined by multiplying the number of balls by the mean volume of balls and subtracting it from the original volume of the dung (the assumed volume of 1kg of dung was 1 L). *Scarabaeus sacer* involved in ball production and rolling were not subjected to any measurements because handling causes them to abandon their balls and the intention of the study was to minimize interference with their feeding routine.

3.3.1 Statistical analysis

When data was not homogeneous, a square root transformation was applied before ANOVA. Duncan's Multiple Range Test was used to compare the mean abundances of the dung dwelling and tunnelling guilds of dung beetles, which are given with standard error (SE). Regression analysis was employed to model the relationship

between dung weight and i) the number of balls produced, ii) the number of balls produced per 100g and iii) ball volume. The SPSS 13.0 package was used for all analyses.

3.4 Results

Scarabaeus sacer produced balls from all 5 sizes of standardised dung pads from 125 g to 2,000 g. A total of 109 balls were produced from 28 of the 30 pads, with the number of balls from individual pads ranging from 0 to 11. Production was highly concentrated, with sixty six balls (61%) produced from 8 of the 30 pads (Figs. 3.1, 3.2). Those 8 pads weighed 500 g, 1,000 g or 2,000 g and mean production was 8.3 balls/pad, compared with1.4 balls/pad from the remaining 10 pads in those 3 pad sizes. The total number of balls produced from the 6 replicates ranged from 9 (250 g pads) to 35 (1,000 g pads). The mean number of balls produced and pad size were significantly related (P < 0.05), with ball production ranging from 1.50 ± 0.62 in 250 g pads to 5.83 ± 1.70 in 1,000 g pads (Table 3.1).

Regression analysis yielded a quadratic equation for the relationship between pad size and number of balls (P < 0.01) and gave a pad weight of 1,371 g for maximum ball production (Fig. 3.2). The fitted curve showed that the number of balls produced per 100 g of dung decreased with increasing pad size (P < 0.01) (Fig. 3). At the extreme pad sizes, *S. sacer* produced more than five times as many balls per unit of dung mass from the smallest pads (125 g; 1 ball/75 g) as from the largest pads (2,000 g; 1 ball/400 g).

The volume of the 30 balls measured from the 5 pad sizes ranged from 16 cc to 86 cc. Mean ball volumes for different pad weights were significantly different (P < 0.05) (Table 3.2). Regression analysis yielded linear, quadratic and cubic equations that described the relationship (P < 0.05), with the quadratic equation providing the best fit (F= 5.060; P = 0.014) (Fig. 4). From the same equation, pad weight for maximum ball volume was 1,260 g. The largest balls and highest number of balls were produced from the 1,000 g pads but the highest percentage utilisation was from the 125 g pads (43%), followed by 1,000 g pads (36%), 500 g pads (29%), 250 g pads (21%) and 2,000 g pads (13%).

Mean ball production/pad/h and time of day were significantly related (P < 0.01); production was almost exclusively nocturnal (98%), with only 2 balls produced outside

night hours (Fig. 5). Fifty nine percent of all ball production was in the period 21.00 to 22.00 over two nights. Many more balls (86 balls; 79% of total) were produced on the first night than on the second night (21 balls; 19% of total) (Figs. 3.1, 3.5).

There was a significant difference ($P < 0.01$) in mean ball production/pad/hour between line 1 (replicates 1, 2 and 3) (0.100 ± 0.02) and line 2 (replicates 4, 5 and 6) (0.051 ± 0.01). Seventy two and 37 balls were produced from lines 1 and 2, respectively, which meant the mean numbers of balls produced/pad from lines 1 and 2 were 4.8 and 2.5, respectively. In contrast, for both lines there was no significant difference in mean ball production/pad/hour between the middle replicate and the two end replicates.

3.5 Discussion

Doube (1990) reported that rollers and large tunnellers are competitively dominant species. *Scarabaeus sacer*, which is a very large roller, was the only roller present during the current study and there were no large tunnellers. This situation represented an opportunity to examine the effects of dung pad size on ball production without the complications posed by the presence of 2 or more dominant species.

Hanski and Cambefort (1991b) reported that the largest dung beetle species are dependent on the largest droppings of the largest herbivores. That was not the case in the current study in which *S. sacer* produced balls from all 5 dung pad sizes (Tables 3.1, 3.2; Figs. 3.1 – 3.4), with 125 g, 250 g and 500 g pads used for ball production while much larger pads were available. Large rollers only need enough dung to make a ball of sufficient size for feeding or breeding so are less restricted by pad size than large tunnellers which generally provision a large nest under the pad with multiple breeding balls and hence require a large initial amount of resource.

The optimum dung pad size for ball production, as determined by curve fitting, was 1,371 g (Fig. 3.2). Peck and Howden (1984) stated that larger baits attracted an order of magnitude more beetles, of nearly double the mean size, than smaller baits. Their finding that larger baits attracted more beetles was corroborated by a key finding of the current study. Errouissi et al. (2004) also reported that large baits in pitfall traps attracted significantly more beetles than small baits. The attraction of larger numbers of individuals to larger baits/pads may be as much related to the strength of odour plumes and attraction distances as to size of the pad/bait per se (P. Giller, pers.

comm.). An additional phenomenon, the aggregation of *S. sacer* at 8 pads of the 3 largest pad sizes, 500 g, 1,000 g and 2,000 g, occurred in the current study. Six times as many balls were produced from these 8 pads as from the remaining 10 pads of those 3 sizes. The presence of glandular structures in male and female *S. sacer* was reported by Pluot-Sigwalt (1994) and they may be responsible for chemical attraction and aggregation. The level of aggregation seen in the present study may be a compromise between intraspecific competition and the probability of encountering potential mates. Furthermore, aggregation at the 8 pads would mean that there was reduced potential for competition at the majority of pads.

In the current study, ball volume ranged from 16 cc to 86 cc. From the fitted curve, the highest ball volume is at 1,260 g (Fig 3.4). In comparison, Marsch (1982) reported that ball size ranged from 12 cc to 70 cc for *S. sacer*. Ybarrondo and Heinrich (1996) reported that competition at the dung pad reduces the size of balls. When dung pads are smaller, the relative density of beetles is higher and they adjust their behaviour to produce smaller brood balls. This is indicative of intraspecific competition (J. Ridsdill-Smith, pers. comm.). In addition, *S. sacer* produces brood, food and nuptial balls (Marsch 1982). Competition at the dung pad and type of ball may therefore have influenced the size of individual balls in the present study.

The highest proportion of dung utilised was from 125 g pads (43%) and the lowest (13%), was from the 2,000 g pads. The highest number of balls was produced from the 1,000 g pads (Fig 3.2) but ball production per 100 g of dung declined steeply as pad size increased (Fig. 3.3). Larger balls were produced from larger pads, with the largest balls produced from 1,000 g pads (Table 3.2; Fig. 3.4). The mean volume of balls produced from the 1,000 g pads was significantly larger than the mean volume of balls produced from the 125 g pads ($P < 0.05$). In addition, the mean volume of balls produced from the 2,000 g and 1,000 g pads was 50% and 70% larger, respectively, than the mean volume of balls produced from the 125 g, 250 g and 500 g pads collectively. This strongly suggests that larger balls are produced from larger pads. However, the use of all five pad sizes for ball production may evidence the availability of sufficient dung to make a ball being *as* important as pad size, e.g., rollers can aggregate sheep pellets into a ball. Separately, an indirect effect of the use of all pad sizes would be a reduction in the level of intraspecies competition, if it is occurring.

Doube (1990) reported that most ball rollers remove dung within approximately 1 hour of arrival at the pad. Results of the current study concur with those of Doube (1990), with most *S. sacer* constructing and rolling balls between 21:00 and 22:00. There was a substantial difference between ball production during that period on the first and second nights, being 52 and 12, respectively (Figs. 3.1, 3.5). That situation probably reflects a reduction in suitability of the pads for ball construction because of desiccation, less volatile compounds to attract *S. sacer*, lower mass of dung due to use by diurnal species, and the presence of fresher, natural pads deposited nearby by free ranging water buffalo, cows and horses.

In a similar but not equivalent experiment, Heinrich and Bartholomew (1979) set out 500 mL pads at 2 h intervals in Kenya to record the arrival times of the large ball roller, *Scarabaeus laevistriatus* Fairmaire. Its 4.5 h activity period commenced at 16.30, peaked approximately 1 h after sunset (18:00) and then tailed off to 21:00. No activity was recorded outside that period.

In Spain, *S. sacer* was active between 21:00 and 11:00, and most active between 24:00 and 2:00, with a substantial peak at 1:00 (Marsch 1982). From a different location in Spain, Verdú et al. (2004) reported the bimodal activity of *S. sacer*, with activity from 5:00 to 10:00 and 17:00 to 22:00, with peaks from 6:00 to 7:00 and at 19:00, respectively. The peak activity period of *S. sacer* in the current study was much more compressed than reported in these two studies (Figs. 1, 5). Marsch (1982) and Verdú et al. (2004) reported the simultaneous presence of *Scarabaeus semipunctatus* Fabricius and *Scarabaeus cicatricosus* (Lucas), respectively, and *S. sacer*. Both species had different peak activity periods to *S. sacer* that reduced the potential for competitive interactions between the species.

The activity period of *S. sacer* in the current study cannot be attributed to phase of the moon or competition with dominant competitor species. The experiment was conducted close to the full moon to assist observer visibility. Peak ball production was close to the period of maximum illumination but *S. sacer* is active during all phases of the moon and in all degrees of illumination at the study site.

Nocturnal activity by *S. sacer* in the area of the current study would likely reduce predation by waterbirds from the nearby wetlands, crows and snakes, but increase exposure to frog, bat, owl and jackal predation. *Scarabaeus sacer* has been reported to be endothermic (Verdú et al. 2004, 2012) but in the present study the increasing

energy costs of ball production as the air temperature fell overnight to 13 ^{o}C may have restricted activity principally to early in the night (21:00 – 22:00) when soil and air temperatures were still relatively high. Mena (2001) reported that dusk flight by *Geotrupes ibericus* Baraud has likely been selectively favoured by vertebrate predation. The optimum period for ball production by *S. sacer* may therefore be a tradeoff between the increased energy costs of ball production at night and the reduced risk of predation at night.

There was a significant difference between the number of balls produced from the 15 pads in lines 1 and 2 ($P < 0.01$). Most Scarabaeinae dung beetles fly upwind to fresh dung pads because they are attracted to their volatile compounds (Inouchi et al. 1988; Dormont et al. 2007). In the current experiment, the most productive line of pads (line 1) was favoured by being more downwind than line 2. In addition, line 1 was closer to a night camp of a large number of water buffalo. *Scarabaeus sacer* may already have been aggregated in that area, waiting buried during the day because of the greater daily availability of fresh dung there.

3.6 Conclusions

Standardised dung pads were a suitable medium for the investigation of the relationship between dung weight and various aspects of ball production by *S. sacer*. The use of a 16-fold range of pad sizes by *S. sacer* demonstrated behavioural variation that may reduce intraspecific competition. Aggregation at particular pads probably further reduces intraspecies competition at other pads. The optimum period for ball production by *S. sacer* may be a compromise between reduced risk of predation at night and the increased energy costs of ball production as the air and soil temperatures fall at night.

3.7 Acknowledgements

Table 3.1 Number of balls produced by *Scarabaeus sacer* L. from five sizes of standardised dung pads in the Kizilirmak Delta of Samsun Province, Turkey

Dung pad weight (g)	Number of balls (Mean ± SE)*
125	1.67 ± 0.33 b
250	1.50 ± 0.62 b
500	4.17 ± 1.08 ab
1,000	5.83 ± 1.70 a
2,000	5.00 ± 1.30 a

*Means with a different letter are significantly different ($P < 0.05$)

Table 3.2 Volume of balls produced by *Scarabaeus sacer* L. from five sizes of standardised dung pads in the Kizilirmak Delta of Samsun Province, Turkey

Dung pad weight (g)	Ball volume (cc) (Mean ± SE)*
125	32.43 ± 7.92 b
250	35.15 ± 2.98 ab
500	34.77 ± 9.43 ab
1,000	58.44 ± 7.45 a
2,000	52.16 ± 6.33 ab

*Means with a different letter are significantly different ($P < 0.05$)
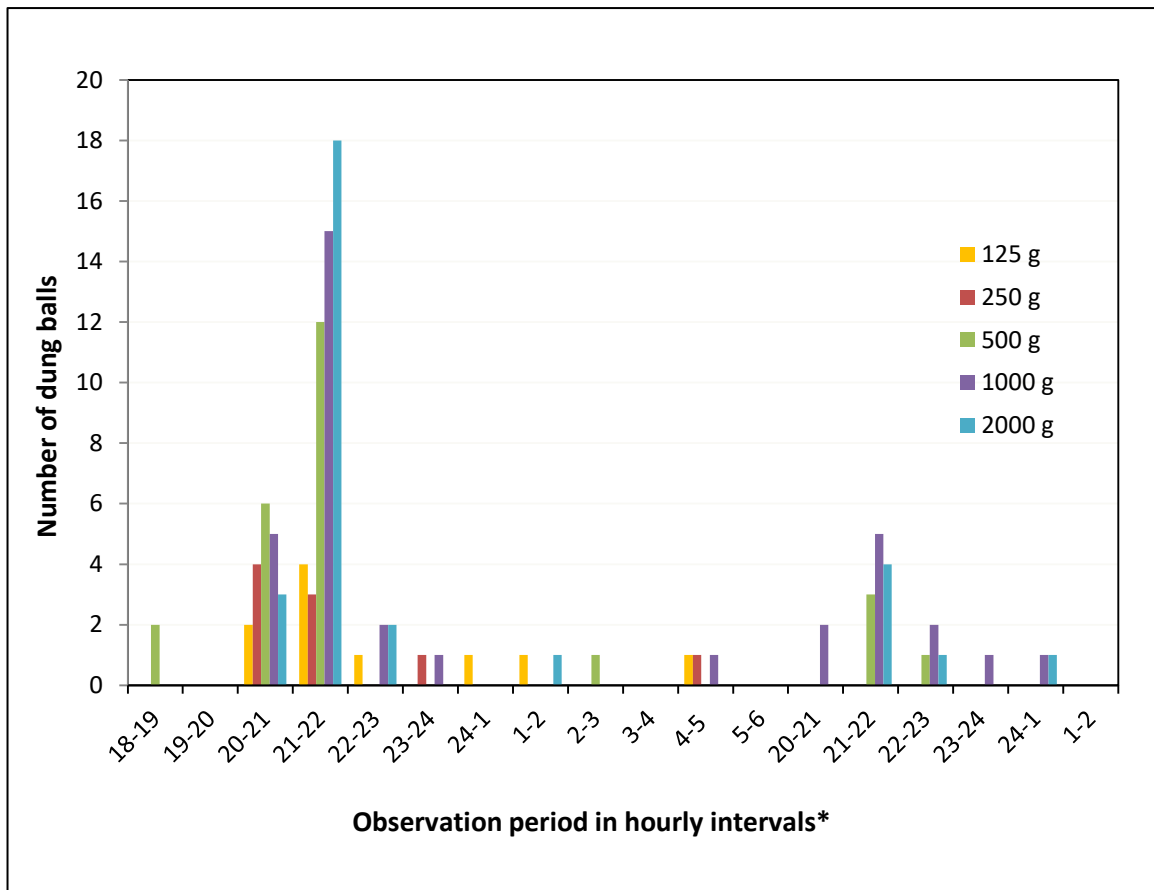
*Most hour periods during which no balls were produced are not included

Figure 3.1 The number of balls produced hourly for 48 h by *Scarabaeus sacer* L. from standardised dung pads in the Kizilirmak Delta on the Black Sea coast of Turkey
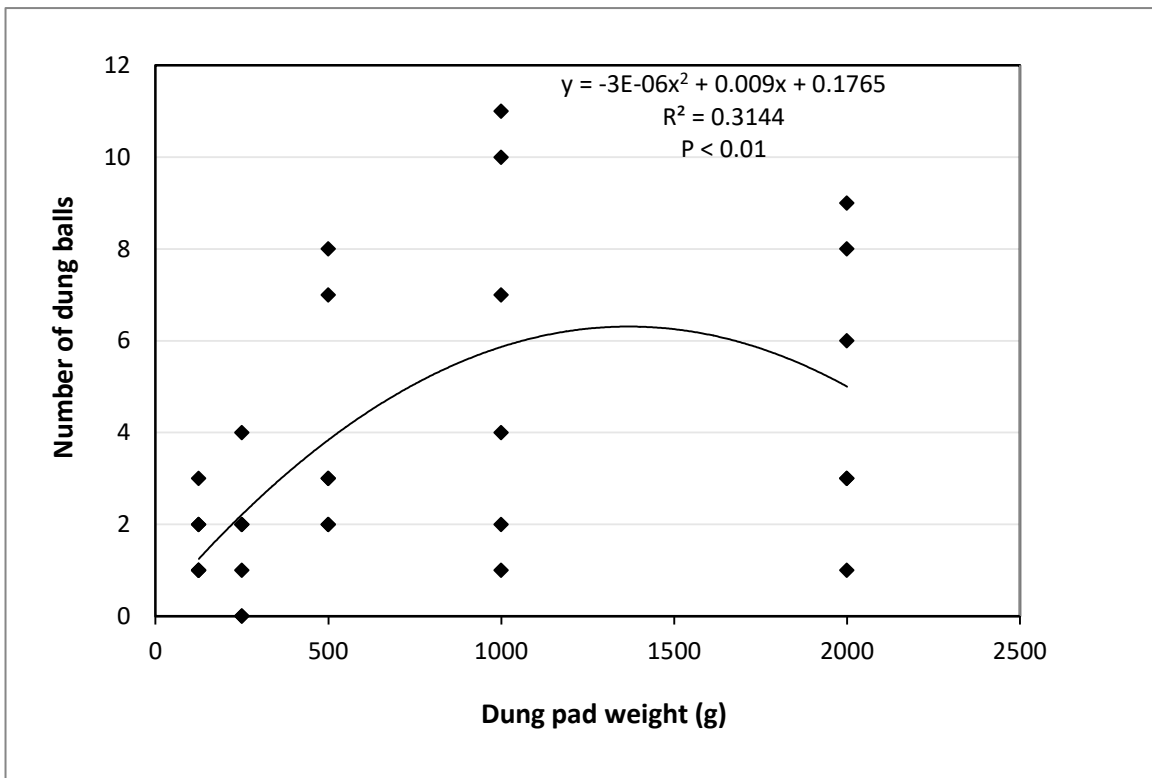
Figure 3.2 Number of balls produced by *Scarabaeus sacer* L. in relation to size of standardised dung pads in the Kizilirmak Delta on the Black Sea coast of Turkey
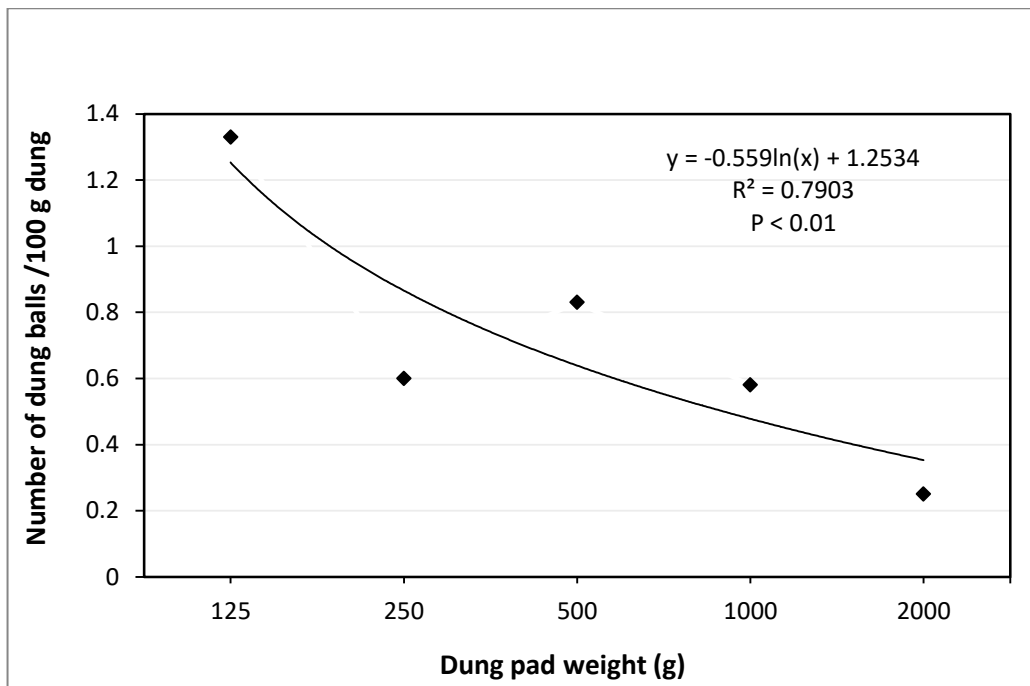
Figure 3.3 Number of balls produced by *Scarabaeus sacer* L. per 100 g of dung in relation to the size of standardised dung pads in the Kizilirmak Delta on the Black Sea coast of Turkey
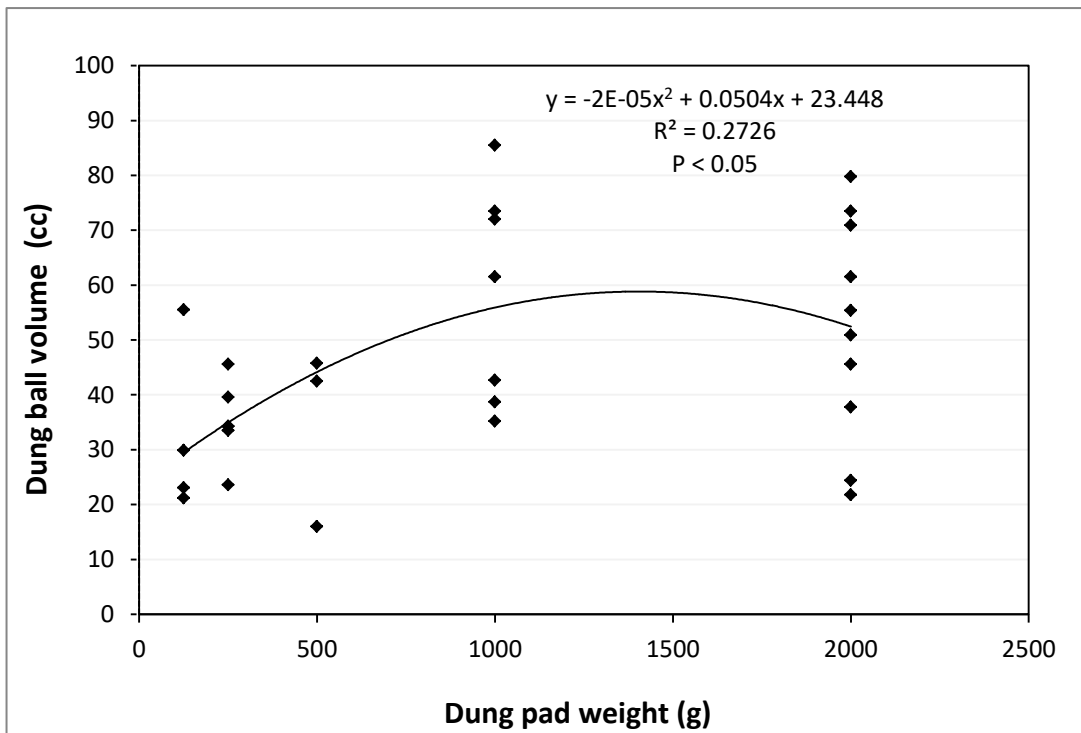
Figure 3.4 Volume of balls produced by *Scarabaeus sacer* L. in relation to the size of standardised dung pads in the Kizilirmak Delta on the Black Sea coast of Turkey
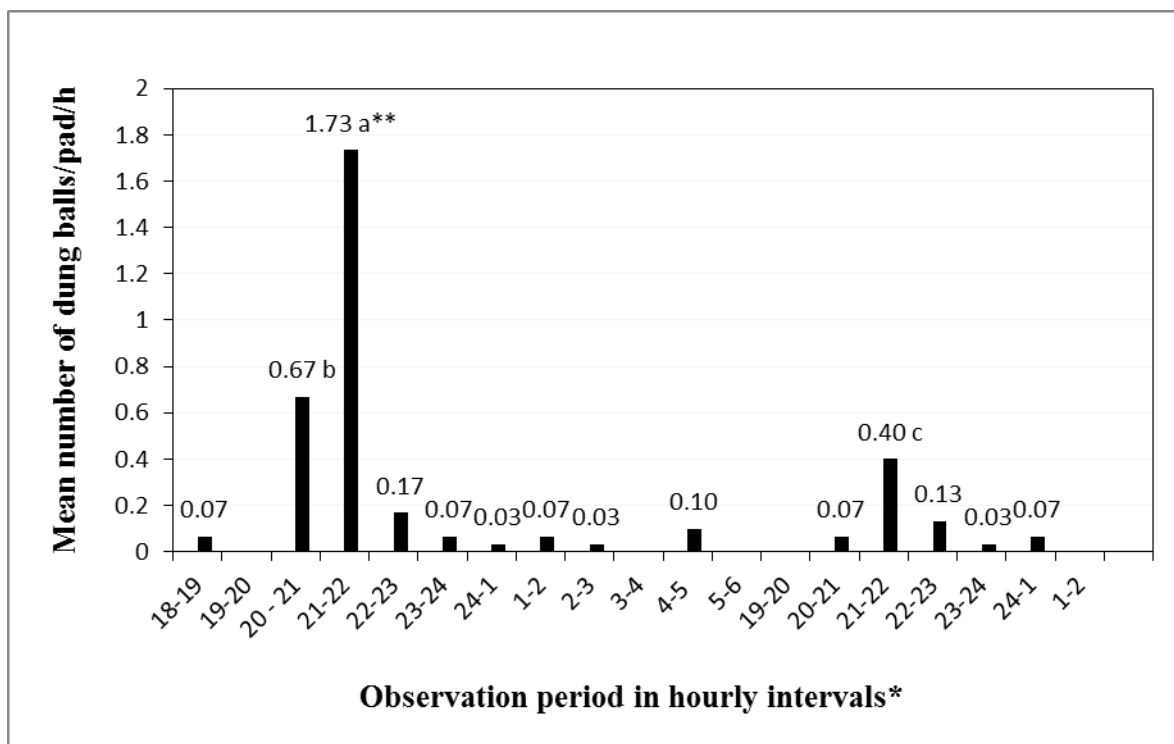
*Most hour periods during which no balls were produced are not included
**Different letters show a significant difference (P < 0.01); means not labelled a, b or c are in group d

Figure 3.5 Number of dung balls produced hourly over 48 h by *Scarabaeus sacer* L. from five sizes of standardised dung pad in the Kizilirmak Delta on the Black Sea coast of Turkey

Plate 10 The dung ball roller *Scarabaeus sacer* L. (Scarabaeidae: Scarabaeinae)

CHAPTER 4 How guilds build success; aspects of resource partitioning in a warm, temperate climate assemblage of dung beetles (Coleoptera: Scarabaeidae)

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4.1 Abstract

Succession in local dung beetle assemblages influences their delivery of ecological functions in natural and modified environments globally. Short term changes in dung beetle (Coleoptera: Scarabaeidae) species richness, abundance and biomass were investigated in standardised dung pads in northern, coastal Turkey. For the mean abundance of tunnelling species, dung deposition time and dung exposure period and their interaction were significant. For the mean abundance of dung dwelling species, dung exposure period was significant, as was the interaction between dung deposition time and dung exposure period. Collectively, these analyses evidenced temporal resource partitioning between the dung dwelling and tunnelling species, based principally on differences in diel activity. Succession was highly compressed, with maximum abundance at 12 h and maximum species richness at 24 h. A large ball roller and small to medium sized tunnellers dominated different periods in the first 24 h but they were superseded by dwellers. Regression analysis demonstrated a significant, positive relationship between species richness and the evenness of

abundance for both dung deposition times. Correlation analysis generally showed strong, positive correlations between tunnelling species, low correlations between tunnelling and dwelling species, and low correlations between dwelling species. Niche partitioning based on size difference (limiting similarity) appears to have acted on the habitat filtering of tunnelling species along the temporal gradient of declining moisture, thereby limiting the number of abundant, concurrent species. The aggregation of tunnelling species provided opportunities for the less competitive dwelling species to occupy less densely populated zones termed temporal refuges. The network of strong, positive correlations between tunnelling species may indicate that their collective functionality is vulnerable to a loss of efficiency if species are lost.

Key words: Aphodiinae, coexistence, ecosystem services, Kizilirmak Delta, Scarabaeinae

4.2 Introduction

Dung beetles provide valuable ecosystem services in natural and semi-natural environments and agroecosystems in temperate, subtropical and tropical latitudes by increasing rates of dung decomposition and nutrient cycling, dispersing seeds and reducing levels of pests of humans and animals (Nichols et al. 2008; Beynon et al. 2012). Early colonisers precondition dung for further colonisation and thus influence the subsequent structure of the community (Valiela 1974). Specifically, heterotrophic succession occurs in dung pads as they age and amongst the earliest colonisers are dung beetles (Doube et al. 1988; Barth et al. 1994; Tixier et al. 2015).

Dung beetle guilds or functional groups employ different nesting strategies: tunnellers produce brood balls in tunnels under dung pads, dung dwellers brood inside the dung pad or at the interface between soil and dung, ball rollers bury dung balls away from the pad, and kleptocoprids use the dung removed from pads by ball rollers and tunnellers (Doube 1990; Hanski and Cambefort 1991c; Krell et al. 2003). The activities of the first three groups have a complementary effect on the rate of dung removal (Beynon et al. 2012), with larger species having a disproportionately larger effect (Rosenlew and Roslin 2008; Nervo et al. 2014).

Doube (1990) proposed a functional classification of seven groups for the analysis of the structure of dung beetle assemblages that is based on the ability of functional groups to compete for the dung resource, with the rollers most competitive, followed

by the tunnellers, and the dwellers least competitive. Different times of dung deposition in a single day, different diel activity periods (day, crepuscular and night) and preferences for dung of different ages reduce the potential for interspecific and interguild competition by providing multiple opportunities for a particular species in a local assemblage to acquire sufficient resource for feeding and breeding purposes, thus promoting coexistence (Montes de Oca and Halffter 1995; Palestrini et al. 1995; Krell et al. 2003; Krell-Westerwalbesloh et al. 2004; Boonrotpong et al. 2012; Sullivan et al. 2016b).

Differences in regional species composition and relative abundance can be expected to occur on the basis of biogeographical processes that generally operate on large spatial and temporal scales, e.g. geographical barriers, climatic differences and historical factors (Finn et al. 1999). Assemblages of dung beetles in the cool, temperate regions of the northern hemisphere are dominated by dung dwelling species (Hanski and Cambefort 1991d; Hutton and Giller 2004). The number of species does not change substantially with decreasing latitude but their abundance is reduced in environments where they are in competition with rollers and tunnellers (Hanski and Cambefort 1991d).

How are dung dwelling species able to persist in environments where they are subject to competition with superior competitors? Krell et al. (2003) refined that question by posing another question: 'Did competitively inferior guilds evolve mechanisms for avoiding or minimizing competition or do they depend on random successes to achieve coexistence with superior competitors'.

There have been studies of colonization and short term succession in dung beetle assemblages in tropical environments where ball rollers and large tunnellers tend to dominate assemblages (Walter 1980; Montes de Oca and Halffter 1995; Krell et al. 2003). In tropical environments, dwellers tend to avoid competition with more competitive species through differences in diel activity or differences in spatial or temporal resource use that result in their accessing dung with lower densities of superior competitors (Krell et al. 2003; Krell-Westerwalbesloh et al. 2004).

In warm, temperate environments, small tunnellers generally dominate assemblages in terms of abundance (Jay-Robert et al. 2008; Anlas et al. 2011a; Sullivan et al. 2017a,b). At two sub-Mediterranean sites in southern France, there were differences in the temporal (seasonal) and spatial use of dung by assemblages that included

dwelling species (Jay-Robert et al. 2008). However, very short term temporal changes in the species richness, abundance and biomass of dung beetles have not been comprehensively investigated in any environment. The current study employed two dung deposition times and seven exposure periods, including four collections in the first 24 h, to investigate whether temporal separation, and by inference, temporal resource partitioning, was occurring in a summer assemblage of warm, temperate climate dung beetles.

4.3 Materials and methods

The experiment was conducted on a coastal sand dune (41° 39′ 26″ N, 36° 04′ 03″ E) in the RAMSAR-listed Kizilirmak Delta in Samsun Province on the central Black Sea coast of Turkey between 15 June and 23 June 2014. Large numbers of free-ranging water buffalo, cattle, horses and sheep graze the extensive sand dune system; the water buffalo also feed on aquatic vegetation in nearby Lake Cernek. The ridge line of the dune on which the experiment was conducted was sparsely covered with low, herbaceous vegetation, predominantly *Euphorbia terracina* L. Sullivan et al. (2016a) reported that the soil at the experiment site was essentially sand that contained a small amount of organic matter. Approximately 70 kg of dung less than 1 h old was collected from the overnight camp of approximately 250 free-ranging water buffalo before 05:00 on June 15, 2014. The individual dung pads were included in the bulking and homogenization process after they were thoroughly checked and determined to be free of insect infestation. The first half of the experiment was established at 06:00. The dung that was not to be used until 18:00 the same day was immediately chilled to 4 °C.

Four, 1 kg samples taken from different sectors of the bulked, homogenized dung were refrigerated at 4 °C until the time of processing. After bulking and homogenizing again, three, 50 g subsamples were oven-dried at 105°C for 24 h. The difference in weight after drying was converted to a percentage moisture loss which was subtracted from 100% to give the dry matter content.

A randomized complete block design was employed for the experiment. Standardised 1 kg dung pads (Rougon and Rougon 1991; Krell 2007) were formed from homogenized water buffalo dung in a plastic mould. They were deposited at two times (06:00 and 18:00) (Krell et al. 2003) and collected after 7 exposure periods (3, 6, 12, 24, 48, 96 and

192 h). A total of 56 experimental pads (2 deposition times x 7 exposure periods x 4 replicates) were used. The four replicates were arranged in two parallel rows, with two replicates in each row. There was 10 m between the rows, 6 m between the replicates, and 5 m between the pads (Sullivan et al. 2016b). The total length of each row was 136 m. At the time of the experiment, the sand was very dry and loose from the surface to 8 to 10 cm depth. However, the sand immediately below the fresh pads gradually dampened through the seepage of moisture from the pad. During the experiment, the air temperature ranged from 15.0 ^{o}C to 28.0 ^{o}C. Fifteen mm of rain fell on the study site on the seventh day, by which time the pads had become hard at the surface and almost dry internally.

At the seven collection times, each pad and 10 cm of sand under the pad were collected. The sand under the pad was collected to capture individuals that had escaped from the pad during its collection or were in tunnels. A modified version of the method of Krell et al. (2003) and Krell (2007) was employed to collect the dung fauna by flotation in water and then sifting through the residues for missed specimens. All specimens were immediately preserved in 96% alcohol until identification.

The large, nocturnal ball rolling species *Scarabaeus sacer* (L.) is present at the study site (Sullivan et al. 2016a,b). Collecting standardised pads when rollers are most active detects them but underestimates their number (Krell et al. 2003). Sullivan et al. (2016b) reported that most *S. sacer* individuals are active at dung pads for a short period at late dusk and into the early night. That meant it is unlikely that *S. sacer* would be present at pads at the designated collection times in the present study. However, as a dominant competitor (Doube 1990), it had to be included in the study. Therefore, all of the dung pads were monitored by two observers who walked along the outside of the two lines of pads at 15 min intervals and at 5 to 10 min intervals during peak ball production periods, using weak torchlight when necessary. To separate users from 'visitors', one dung ball produced was equated to one *S. sacer* for total abundance and biomass purposes (Sullivan et al. 2016b). Monitoring was terminated after 72 h, by which time the dung pads were too desiccated for ball production.

The biomass of individual species was calculated according to a modified version of the methodology of Doube (1990). Thirty randomly selected specimens of each species, with the exception of *Esymus merdarius* (Fabricius) and *Labarrus lividus* (Olivier) (20 specimens), and *S. sacer* (13 specimens), were oven dried for 24 h at 70

^{o}C. Three species, *Bodiloides ictericus* (Laicharting) *ssp. ghardimaouensis* ;, *Onthophagus opacicollis* Reitter and *Onthophagus vacca* (L.), represented by six or less specimens in total, were not included in biomass calculations. Following drying, the bulked specimens of each species were weighed on Precisa XB 629M scales sensitive to 0.001g.

To compare the weight or biomass of dung beetles with the amount of available resource, the total dry weight of dung beetles collected from the 56 experimental pads was converted to a percentage of the total dry weight of dung in the original pads.

Core, satellite and accessory species are defined by the relative importance of their contributions to the ecological functioning of an assemblage at a particular time (Hanski 1982; Stiernet and Lumaret 1993; Kadiri et al. 2014). All species were categorized as core, satellite or accessory, according to whether they constituted: i) >10% of total abundance and >10% of biomass, ii) >10% of total abundance or >10% biomass, or iii) <10% of total abundance and <10% of biomass, respectively (Lumaret et al. 1992; Stiernet and Lumaret 1993; Kadiri et al. 2014).

Dung beetles were identified principally by the third author (J-P. L.) and by the first author (G. T. S.), with the aid of a Leica stereomicroscope (40X magnification) and the keys of Baraud (1985, 1992). Voucher specimens of all species collected are held at the Plant Protection Department of the Faculty of Agriculture, Ondokuz Mayis University in Samsun, Turkey.

4.3.1 Statistical analysis

To investigate temporal resource partitioning, two-way ANOVA in the aov function of R-3.3.0 (R Development Core Team 2013) was used to examine the effects of dung deposition time and exposure period on the mean abundance of the dung dwelling and tunnelling guilds/functional groups of dung beetles. Before the analyses, the data was transformed by taking the square root or double square root to make the variance independent of the mean. Following the analyses, the adjusted LSD test was used to compare the treatment means. To investigate interspecific aggregation, the cor function of R-3.3.0 (R Development Core Team 2013) was used to determine the correlation coefficients of pairs of species across the two dung deposition times and seven dung collection times. The significance levels, which depended on the number of observations, were taken from Fisher and Yates (1963). The ball roller *S. sacer* was

active at some of the dung pads but not at the specific dung collection times; it was the subject of a separate study (Sullivan et al. 2016b). The relationship between species richness and relative abundance or evenness (1/d), where d = Berger - Parker dominance index, was determined by regression analysis (Berger and Parker 1970; Davis 1993). The SPSS 13.0 package was used for the regression analysis.

4.4 Results

A total of 2,899 adult dung beetles from one family, two subfamilies, 12 genera and 18 species were collected. The dung dwellers, *E. merdarius* and *Planolinellus vittatus* (Say) (Table 4.1), are additional to the species reported from the Kizilirmak Delta by Sullivan et al. (2016a, 2017). There were eight genera and four genera from the subfamilies Aphodiinae and Scarabaeinae (Scarabaeidae), respectively. Three guilds, namely tunnelling, dwelling and ball rolling, were represented by 10, seven and one species, respectively. Tunnellers, dwellers and the ball roller constituted 60.7%, 35.5% and 3.8%, respectively, of all individuals collected. *Caccobius schreberi* (L.)*, Subrinus sturmi* (Harold) and *Onthophagus taurus* (Schreber) contributed 24.2%, 20.9% and 10.4%, respectively, of all individuals (Table 4.1). The percentages of the total abundance of all dung dwelling and tunnelling species for all dung deposition times and exposure periods are provided in Table 4.2.

The total number of dung beetles collected from the 06:00 pads was 36% higher than from the 18:00 pads. There were nearly 3 times as many tunnellers as dwellers in the 06:00 pads. The total number of tunnellers in the 06:00 pads was twice that in the 18:00 pads. However, there were almost equal numbers of both guilds in the 18:00 pads, including 50% more dwellers than in the 06:00 pads (Tables 4.1, 4.2). Each of the10 tunnelling species was more numerous in the 06:00 pads, six of the seven dung dwelling species were more numerous in the 18:00 pads, and the ball roller *S. sacer* was 68% more abundant at the 18.00 pads (Table 4.1). The peak numbers of the two most numerous tunnellers, *C. schreberi* and *O. taurus,* were earlier and their mean numbers were higher in the 6.00 pads. The mean abundance of the most common dweller, *S. sturmi*, which was higher in the 18:00 pads, peaked at 48 h and 96 h in the 06:00 pads and 18:00 pads, respectively (Fig. 4.1, Tables 4.1, 4.2). The same trends were evident in the biomass comparisons (Fig. 4.2).

There were distinct temporal changes in the species richness, abundance and biomass of dwelling and tunnelling dung beetles. Species richness peaked at 16 at 24 h for both dung deposition times and abundance peaked at 12 h and 24 h for the 06.00 and 18.00 dung deposition times, respectively (Table 3). In the current study, four species contributed 59.3% of all specimens and 93.6% of the dry biomass; *S. sacer* contributed 3.8% of all specimens and 83.3% of biomass; *C. schreberi* and *O. taurus* contributed the most individuals and biomass, respectively, of the tunnellers; and *S. sturmi* was the most numerous dwelling species (20.1% of all individuals) but it contributed only 0.5% of all biomass (Tables 4.2, 4.3; Figs 4.1, 4.2). Collectively, the tunnellers and dwellers contributed 15.2% and 1.5% of biomass, respectively, of the total biomass. The only core species was *O. taurus* (> 10% of abundance and biomass); the satellite species were *S. sacer* (> 10% of biomass), and *C. schreberi* and *S. sturmi* (> 10% of abundance); and the remaining 14 species were accessory species.

For tunneller abundance, there was significant interaction between dung deposition time and exposure period; i.e., they were not independent, and both factors were also significant (interaction: F = 3.50, df = 4, 30, P < 0.05; deposition time: F = 18.2, df = 1, 30, P < 0.001; exposure period: F = 8.60, df = 4, 30, P < 0.01). For dweller abundance, there was significant interaction and exposure period was significant but deposition time was not significant (interaction: F = 2.87, df = 5, 36, P < 0.05; exposure period: F = 33.77, df = 5, 36, P < 0.001; dung deposition time: F = 2.02, df = 1, 36, NS) (Table 4.4).

Among the 70 possible pairings between the dung dwelling and tunnelling species, correlation analysis showed eight significant, negative correlations and five significant, positive correlations. Mean tunneller abundance was significantly, negatively correlated with mean dweller abundance (P < 0.05). Furthermore, there were significant, negative correlations between mean dweller abundance and the most abundant tunnelling species, *C. schreberi* (P < 0.001) and the highest dry biomass tunnelling species, *O. taurus* (P < 0.05). In a specific case, the most abundant dweller, *S. sturmi*, was significantly, negatively correlated with the most abundant and highest biomass tunnelling species, *O. taurus* (P < 0.01, r = - 0.39) (Table 4.5).

In total, there were 45 and 21 possible pairings between the ten tunnelling species and between the seven dung dwelling species, respectively. Among the tunnellers, there

were 24 significant, positive correlations, with 16 significant at P < 0.001, and no significant, negative correlations. Among the seven most common tunnellers, 14 of the 21 correlations were at P < 0.01 or P < 0.001. The only aphodiid tunneller, *Colobopterus erraticus* (L.), was significantly, positively correlated with three of the four most common tunnellers. In contrast, there were only four significant, positive correlations among the seven dwellers but as with the tunnellers, there were no significant negative correlations. On a proportional basis, there were nearly three times more significant, positive correlations between tunnellers than between dwellers, with none of the correlations among the dwellers at P < 0.001 (Table 4.5).

The relationship between species richness and abundance was examined through regression analysis which demonstrated a significant, positive relationship (P < 0.01) between species richness and the evenness of abundance, i.e., the reciprocal of the Berger - Parker dominance index (1/d)), for both the 06:00 and 18:00 dung deposition times (Figs. 4.3 A,B). In other words, as the number of species increased, a particular species or set of species was less likely to dominate total abundance.

The total dry weight or biomass of ball rolling, dwelling and tunnelling dung beetles collected in this study was 99.5 g, of which *S. sacer* contributed 83.3%. Tunnellers contributed the second to seventh highest dry biomass totals, with the dung dweller *Otophorus haemorrhoidalis* L. in eighth position. The total dry biomass of *S. sacer* was five times greater than all the tunnellers combined (15.2%) and dwellers combined (1.5%). Furthermore, its dry biomass was 14.7 times greater than that of the next highest species, the tunneller *O. taurus* (5.7%), 136 times that of the highest biomass dweller, *O. haemorrhoidalis* (0.6%), and 2,720 times that of *E. merdarius* (0.03%), the dweller that contributed least biomass.

The total wet weight of the original 56 dung pads was 56 kg, their moisture content was 83.6% and dry matter content was 9,200 g (16.4 %). The total dry biomass of the collected dung beetles (99.5 g) was 1.1% of the total dry biomass of the dung pads (9,200 g) at the start of the experiment.

4.5 Discussion

The current study investigated short-term, temporal changes in species richness, abundance and biomass in a summer dung beetle assemblage at the Kizilirmak Delta on the northern, Black Sea coast of Turkey. In such warm, southern temperate climate

dung beetle assemblages, the small tunnellers generally dominate abundance (Hanski and Cambefort 1991d; Jay-Robert et al. 2008; Anlas et al. 2011a). In the present study, the tunnellers contributed the majority (61%) of individuals. With the exception of the tunneller, *C. erraticus* (Rojewski 1983), the Aphodiinae are all dwellers, and the Scarabaeinae are tunnellers, except for the ball roller, *S. sacer*, which buries its ball away from the dung pad.

In the present study, succession was highly compressed, with dung beetle abundance peaking at 12 h and 24 hours in the 06:00 and 18:00 pads, respectively (Tables 4.3, 4.4). The rapid transition from dominance by the tunnellers to the dwellers was exemplified by the population trends of the two most common tunnellers and the most common dweller (Figs 4.1, 4.2). From northern temperate Finland, Koskela and Hanski (1977) reported a peak in the numbers of coprophages in the first 24 to 48 hrs. Rougon and Rougon (1991) reported that on sand during the warm, dry season in Niger in north-central Africa, where extreme microclimatic conditions cause rapid dehydration of pads, the temporal sequence of colonization is greatly accelerated and the maximum number of dung beetles is reached during the first day, a situation akin to the current study. Sladecek et al. (2017) reported that communities of species inhabiting ephemeral habitats such as dung show temporal distributions along three axes, namely diel/daily activity, succession and seasonality. Furthermore, they reported that both habitat filtering, the co-occurrence of potential competitors along the successional gradient, based on similar environmental tolerances, and niche separation, are able to shape these temporal distributions. The significant effects of dung deposition time and exposure period and their interaction on mean guild abundance in the present study evidenced temporal separation and by inference, temporal resource partitioning, which is attributable to diel activity (Hernandez 2002; Boonrotpong et al. 2012), interspecific aggregation patterns (Hutton and Giller 2004), size differences (Lumaret et al. 1992) and changes in dung quality over time (Doube et al. 1988; Lumaret and Stiernet 1991). The tunnellers preferred the dung deposited at 06:00 because it was fresh during their peak flight period in the morning. By the time they flew again in peak numbers the following morning, there were fresh, natural dung pads in the vicinity of the study area. Lumaret (1995) reported that the dwellers generally prefer older dung because moisture conditions are more suitable and there is less competitive interference by tunnellers. Most of the dwellers collected in the

current study were *S. sturmi*, with most arriving when the numbers of other species and their abundance had declined.

In the current study, the tunnellers, which were mainly active during daylight hours, especially in the morning (Tables 4.2 – 4.4), were numerically overtaken by dwellers between 24 h and 48 h after dung deposition, and the total transition was almost complete at 96 h (Tables 4.3 – 4.5). By that time, the dung pads had become very desiccated, except in the centre and at the pad-sand interface. Separately, dung deposited at 18:00 attracted a much higher proportion of dwellers than dung deposited at 06:00 (Table 4.1). Both situations may indicate avoidance of competition by the dwellers, which were crepuscular/night active, except for day active *O. haemorrhoidalis* and day/night active *P. vittatus.*

The large ball roller *S. sacer*, which is categorized as a dominant competitor (Doube 1990, 1991), has been reported as nocturnal (Marsch 1982; Baraud 1992; Sullivan et al. 2016b, 2017a). There was nearly 70% more ball production by *S. sacer* from the 18:00 pads than from the 06:00 pads (Table 4.1). That may have been a consequence of the 18:00 pads having suitable moisture content during the peak ball production period (21:00 – 22:30) on two consecutive nights, as opposed to one peak ball production period for the 06:00 pads before the dung became too dry. However, *S. sacer* removed a relatively small proportion of pads deposited at both 06:00 and 18:00. Furthermore, its activity was concentrated on a small proportion of pads, as reported by Sullivan et al. (2016b), which may have further reduced overall levels of disturbance of tunnellers and dwellers. Krell-Westerwalbesloh et al. (2004) also reported a distinct pattern of diel activity by dwellers and tunnellers that reduced competition with ball rollers in a tropical forest-savanna mosaic in the Ivory Coast in Africa.

Biological traits, including size of species, spatio-temporal reproductive patterns and life history, play a major role in facilitating the co-existence of different species in an assemblage (Lumaret et al. 1992; Kadiri et al. 2014). Giller and Doube (1994) reported that the coexistence of guilds is promoted by the increased aggregation of competitively superior species, resulting in less populated or vacant sites in which less competitive species can breed. In the present study, the separate temporal aggregation of the tunnelling species (Table 4.1) and ball roller would have resulted in pads or parts of pads with lower densities of these superior competitors for the dwelling species (inferior competitors) to occupy, thereby increasing the dwellers

relative competitiveness and breeding opportunities. Such less densely populated sites were termed probability refuges by Shorrocks and Rosewell (1987) and temporal refuges by Krell-Westerwalbesloh et al. (2004).

In the current study, the total dry biomass of all the dung beetles collected was just over 1% of the total dry weight of the original dung pads and there was a very large surplus of dry, unused dung after total abandonment of the pads by adults. Non-saturation of the dung resource by the dung beetle community (Horgan 2006) may therefore be an additional factor reducing competition among the three guilds and facilitating their coexistence. Alternatively, Ridsdill-Smith (1991) reported that intraspecific interference competition can occur between beetles in pads long before any shortage of dung generates exploitation competition; this may explain, in part or in full, why Sullivan *et al.* (2016b, 2017a) reported large amounts of unused dung across 3 field experiments. Furthermore, Palestrini et al. (1998), Hartley and Shorrocks (2002), Hutton and Giller (2004) and Horgan (2006) have reported on the effects of intraspecific and interspecific aggregation on competition, coexistence and biodiversity. From a different environment, Cardinale et al. (2002) reported that increasing the species diversity of a functional group of aquatic organisms induces facilitative interactions and non-additive changes in resource consumption.

In the current study, the overall pattern of correlations or aggregations among the tunnellers and dwellers (Table 4.5) was in strong agreement with the pattern in a study conducted by Sullivan et al. (2017a) in the late summer of 2015 at the same site that employed six dung deposition times (06.00, 10.00, 14.00, 18.00, 22.00 and 02.00) during a 24 h period and three dung collection times (12, 24 and 48 h). In the 2015 study, the tunnelling species showed a very strong tendency to associate positively, and the dwelling species tended, except for *O. haemorrhoidalis*, not to associate with the tunnelling species. The abundances of individual species varied widely between 2014 and 2015 and some species were collected only in 2014 or 2015. Correlations between the same species in 2014 and 2015 ranged from almost the same to considerably different. However, the same overall patterns of intraguild and interguild correlations were evident.

Hanski (1982) stated that if the coexistence and dominance of competing species is dependent on their size relative to the size of other species, the most dominant species should be more evenly spaced in size than a random selection of species.

Supporting evidence was provided by Lumaret et al. (1992) who reported that the coexistence of abundant species in the same guild is dependent on their being in different size classes. In the present study, the five most abundant tunnelling species, *C. schreberi*, *O. taurus*, *O. ruficapillus*, *O. furcatus* and *E. pallipes*, represented 51% of all dung beetles collected (Tables 4.1, 4.5). In descending order of abundance, these 5 species belonged to the size classes 3 (5 - 8 mg), 5 (17 - 32 mg), 2 (3 - 4 mg), 2, and 4 (9 - 16 mg) of Lumaret et al. (1992), supporting the assertion of Hanski (1982) and Lumaret et al. (1992) that size difference is a necessary condition for the co-occurrence of abundant species.

Hanski and Cambefort (1991b) reported a similar phenomenon in guilds of rollers and termed it 'limiting similarity'. Cambefort (1991b) reported that as the size difference between two species increases, the level of competition decreases. Concurrent diel activity and then habitat filtering along the temporal moisture gradient as the pads dried could account for the co-occurrence of the five abundant species of tunnellers. Furthermore, niche partitioning based on size difference, referred to as 'limiting similarity' by Cambefort (1991b), appears to have affected habitat filtering by restricting the number of tunnelling species that could be both concurrent and abundant.

A different perspective on interspecific relationships is provided by the Berger - Parker dominance index. In the current study, logarithmic regression analysis of the relationship between relative abundance or evenness (inverse of the Berger - Parker dominance index = 1/d) and species richness revealed a significant, positive relationship (Figs 4.3 A,B), as reported in a coprophilous South African assemblage by Davis (1993). In essence, as the number of species in a set of pads increased, the degree of dominance of abundance by any species or group of species decreased.

Core and satellite species define the functional group at a given time within an assemblage (Hanski 1982). In the current study, based on the definitions of Lumaret et al. (1992) and Stiernet and Lumaret (1993), there was only one core species and three satellite species. Core species, or keystone species, are of demonstrable importance for ecosystem function (Cottee-Jones and Whittaker 2012). Some of the 14 accessory species, in other seasons, especially given the relatively warm winters in the study area, may achieve the status of satellite or core species. Lumaret and Stiernet (1992) reported that status changes can be rapid, especially in the mountains, where within a

few weeks a species can shift from being a core species to a satellite or accessory species, or vice versa. Furthermore, Beynon et al. (2012) suggested that apparently redundant taxa may be critical to sustaining ecosystem functions and services in altered environments.

Knowing the abundance of a species, which depends on the quantity of trophic resources available, is useful (Lumaret et al. 1992) but results expressed as biomass provide a better perspective on the ecological role of species (Kadiri et al. 2014; Chamberlain et al. 2015) because the amount of dung consumed is directly related to biomass (Nervo et al. 2014). Doube (1991) reported that in southern Africa on sandy soils with a bush-grass mosaic, large rollers may account for 80-90% of biomass. In the current study, which was conducted on a sand dune adjacent in the Kizilirmak Delta in northern Turkey, the percentage of the total biomass contributed by the large ball roller *S. sacer* was in the range reported by Doube (1991).

In the overwhelming majority of dung beetle assemblages in temperate and Mediterranean regions, including montane areas, three or four species contribute about 80% of the biomass or abundance of dung beetle assemblages (Lumaret and Stiernet 1991, 1994; Jay-Robert et al. 2008; Sullivan et al. 2017a). In the present study, the mean dry biomass of *S. sacer* individuals was approximately 40 times that of the largest tunneller, *O. taurus*. Although they are primarily active at the same time, *O. taurus* is 3.5 times larger than the much more numerous tunneller, *C. schreberi*. The dweller *S. sturmi*, which is approximately one-fifth the size of the smallest tunneller, *Onthophagus furcatus* Fabricius, minimised potential competition with the other, much larger core and satellite species by generally using older dung, especially dung deposited at 18:00 (Figs 4.1, 4.2). Cambefort (1991b) reported that the larger the species, the more dominant it is in terms of biomass (P < 0.001) and that there is a negative correlation between weight and abundance (P < 0.01). The results of the current study are in agreement with those of Cambefort (1991b).

4.6 Synthesis

In the present study of a warm temperate climate assemblage of dung beetles, succession was highly compressed. This phenomenon, which mirrored some characteristics of subtropical and tropical environments, evidenced temporal resource partitioning. However, a critical difference between the site for the current study and

tropical environments (Krell et al. 2003) was the relatively low number of rollers and the absence of large tunnellers that can rapidly reduce the volume of the dung resource at the former. That situation provided a potentially less competitive environment for the small and medium-sized tunnellers, and dwellers. Overall, the harsh microclimatic conditions at the dung pad surface contributed to rapid dung dehydration and accelerated temporal succession. The presence of the single large ball roller in relatively low numbers, the absence of large tunnellers and the rapid drying of the dung probably contributed to the non-use of a high proportion of the original dung mass.

In the current study, dung beetle species showed distributions along two temporal axes, namely diel/daily activity and succession, of the three temporal axes reported by Sladecek et al. (2017). Diel activity and then habitat filtering appear to be the main factors that drove the initial aggregation of the tunnelling species in the dung pads in the current study. Subsequently, niche partitioning based on size difference, i.e. limiting similarity, appears to have acted on habitat filtering by restricting the number of co-occurring, abundant tunnelling species. This aggregation of tunnelling species would have provided opportunities for the less competitive species of the dung dwelling guild to occupy less densely occupied zones termed temporal refuges by Krell-Westerwalbesloh et al. (2004). Non-saturation of the dung resource by the dung beetle community (Horgan 2006) may also have reduced the potential for competition among the three guilds, thereby facilitating their co-occurrence.

Temporal resource partitioning between the ball rolling, tunnelling and dwelling guilds, which was apparently attributable to differences in their diel activity, aggregation patterns and in the age of dung preferred, reduced the potential for interguild competition and may promote coexistence and the maintenance of diversity. However, the network of strong, positive correlations between tunnelling species suggests that the collective functionality of that guild is vulnerable to a loss of efficiency if a species is lost.

4.7 Acknowledgements

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Table 4.1 Abundances of dung beetles in standardised dung pads exposed for seven different periods in the Kizilirmak Delta of Samsun Province, Turkey

Subfamily	Species	Guild	Number of specimens			
			06.00 deposition	18.00 deposition	Total	% of total
	Acanthobodilus immundus (Creutzer)		2	33	35	1.21
	Bodiloides ictericus ssp. *ghardimaouensis* Balthasar		0	3	3	0.10
Aphodiinae	*Esymus merdarius* (Fabricius)	Dweller	3	20	23	0.79
	Labarrus lividus (Olivier)		6	23	29	1.00
	Otophorus haemorrhoidalis (L.)		114	112	226	7.80
	Planolinellus vittatus (Say)		51	56	107	3.69
	Subrinus sturmi (Harold)		252	355	607	20.9
	Colobopterus erraticus (L.)	Tunneller	45	13	58	2.00

	Caccobius schreberi (L.)		417	283	700	24.15
	Euoniticellus fulvus (Goeze)		73	25	98	3.38
	Euoniticellus pallipes (Fabricius)		82	40	122	4.21
	Onthophagus furcatus (Fabricius)		138	21	159	5.48
Scarabaeinae	*Onthophagus nuchicornis* (L.)	Tunneller	66	44	110	3.79
	Onthophagus opacicollis Reitter		4	2	6	0.21
	Onthophagus ruficapillus Brullé		140	59	199	6.86
	Onthophagus taurus (Schreber)		208	94	302	10.42
	Onthophagus vacca (L.)		4	1	5	0.17
	Scarabaeus sacer L.	Ball roller	41	69	110	3.79
	Total		1,646	1,253	2,899	100

Table 4.2 Percentages of dung beetle species in standardised dung pads in the Kizilirmak Delta in Samsun Province, Turkey

Species	Abundance of individual species (%)*														
	6:00 dung deposition								18:00 dung deposition						
	Exposure period (h)							**Total**	Exposure period (h)						**Total**
	3	6	12	24	48	96	192		3	6	12	24	48	96	192	
Acanthobodilus immundus (Creutzer)	0	0	0	0.69	0	0	0	**0.12**	4.65	5.10	8.99	0.54	5.06	0	0	**2.79**
Bodiloides ictericus ssp. *ghardimaouensis* (Balthasar)	0	0	0	0	0	0	0	**0**	0	0	1.12	0.27	0.42	0	0	**0.25**
Esymus merdarius (Fabricius)	0.44	0	0	0.34	0.35	0	0	**0.19**	1.55	4.08	7.86	0.81	1.69	0	0	**1.69**
Labarrus lividus (Olivier)	0	0	0	0.69	1.41	0	0	**0.37**	6.20	1.02	3.37	2.96	0	0	0	**1.94**
Otophorus haemorrhoidalis (L.)	0	6.22	6.25	9.31	14.08	0	0	**7.10**	0	0	0	11.59	21.10	7.31	0	**9.47**
Planolinellus vittatus (Say)	2.21	1.08	2.86	4.83	5.99	0	0	**3.18**	6.98	4.08	8.99	4.58	5.49	1.92	0	**4.73**
Subrinus sturmi (Harold)	0	0	0	12.41	58.45	100	0	**15.70**	1.55	1.02	2.25	0.27	48.52	90.00	0	**29.98**
Colobopterus erraticus (L.)	3.10	1.89	1.82	6.21	2.11	0	0	**2.80**	0	0	0	2.16	1.69	0.38	0	**1.10**
Caccobius schreberi (L.)	51.33	33.78	28.91	16.21	5.99	0	100	**25.98**	53.49	60.20	57.30	23.18	7.17	0.38	0	**23.90**
Euoniticellus fulvus (Goeze)	1.33	8.92	6.51	3.44	0.70	0	0	**4.55**	0	1.02	0	6.20	0.42	0	0	**2.11**
Euoniticellus pallipes	1.33	5.95	5.21	7.93	4.93	0	0	**5.11**	2.33	5.10	0	8.36	0.42	0	0	**3.38**

(Fabricius)															
Onthophagus furcatus (Fabricius)	7.96	13.51	10.42	9.66	0.70	0	0	**8.60**	0.78	0	1.12	5.12	0	0	0	**1.77**
Onthophagus nuchicornis (L.)	5.31	3.24	8.33	3.10	0.35	0	0	**4.11**	13.95	7.14	4.49	3.77	0.42	0	0	**3.72**
Onthophagus opacicollis Reitter	0	0	0.26	1.03	0	0	0	**0.25**	0.78	0	1.12	0	0	0	0	**0.17**
Onthophagus ruficapillus Brullé	9.29	7.30	11.72	13.80	2.46	0	0	**8.72**	0.78	0	0	11.05	7.17	0	0	**4.98**
Onthophagus taurus (Schreber)	17.70	18.11	17.45	9.66	2.11	0	0	**12.96**	6.98	11.22	3.37	18.87	0.42	0	0	**7.94**
Onthophagus vacca (L.)	0	0	0.26	0.69	0.35	0	0	**0.25**	0	0	0	0.27	0	0	0	**0.08**
Total number of specimens	226	370	384	290	284	50	1	**1605**	129	98	89	371	237	260	0	**1184**

*The columns in the sub-tables show the percentage (%) for each dung beetle species as a % of total abundance for that exposure period; the final, bolded column shows the % for each species as a % of total abundance for all exposure periods combined. The ball roller, *Scarabaeus sacer*, was not included because it was not present at pads at the specific dung collection times

Table 4.3 Temporal changes in the species richness, abundance and biomass of dwelling and tunnelling dung beetles in standardised dung pads in the Kizilirmak Delta in Samsun Province, Turkey

Dung deposition time	Exposure period (h)	No. of species	No. of individuals	(%) of total	Most abundant species*	Highest biomass species*
	3	10	226	14.1	Cs	Ot
	6	10	370	23.1	Cs	Ot
	12	12	384	23.9	Cs	Ot
	24	16	290	18.1	Cs	Ot
	48	14	284	17.7	Ss	Ep
6:00	96	1	50	3.1	Ss	Ss
	192	1	1	0.1	Cs	Cs
	Total	16	1,605	100	Cs = 417	Dry wt. of Ot (208 individuals) = 3.89 g
	3	12	129	10.9	Cs	Cs
	6	10	98	8.3	Cs	Cs
	12	11	89	7.5	Cs	Cs
	24	16	371	31.3	Cs	Ot
18.00	48	13	237	20.0	Ss	Oh
	96	5	260	22.0	Ss	Ss
	192	0	0	0	-	-
	Total	17	1,184	100	Ss = 355	Dry wt. of Ot (94 individuals) = 1.76 g

*Aphodiinae (dwellers): Oh = *Otophorus haemorrhoidalis* (L.), Ss = *Subrinus sturmi* (Harold); Scarabaeinae (tunnellers): Cs = *Caccobius schreberi* (L.), Ep = *Euoniticellus pallipes* (Fabricius), Ot = *Onthophagus taurus* (Schreber)

Table 4.4 Abundances (mean ± SE) of dwelling and tunnelling dung beetle species in standardised dung pads in the Kizilirmak Delta in Samsun Province, Turkey

	Tunnelling species			Dwelling species	
Exposure period (h)	Dung deposition time		Exposure period (h)	Dung deposition time	
	6:00	18:00		6:00	18:00
3	56 ± 6 ab*	26 ± 7 bc	3	1.5 ± 1 d	6.8 ± 3 c
6	86 ± 17 a	21 ± 4 bc	6	6.8 ± 2 c	3.8 ± 2 cd
12	87 ± 20 a	15 ± 6 bcd	12	8.8 ± 3 c	7.3 ± 1 c
24	52 ± 12 ab	73 ± 9 a	24	20 ± 6 b	20 ± 4 b
48	14 ± 3 bcd	10 ± 4 d	48	57 ± 6 a	49 ± 12 a
96	0	0.5 ± 0.5	96	13 ± 10 c	65 ± 22 a

*Within the tunnelling and dwelling species sub-tables, means followed by the same letter are not significantly different (Tukey's HSD, $P < 0.05$). Means are on the untransformed scale but significance is from the transformed analyses. The 96 hour exposure period data for tunnellers was excluded from the analysis and 192 h was excluded for both tunnellers and dung dwellers (only 1 specimen was collected at 192 h)

Table 4.5 Correlation coefficients of dwelling and tunnelling species of dung beetles in standardised dung pads in the Kizilirmak Delta in Samsun Province, Turkey

	Cs	Ot	Or	Of	Ep	On	Ef	Ce	Oo	Ov	tot.t	Ai	Bg	Ss	Pv	Em	Ll	Oh	tot.d
Cs	1.0																		
Ot	<u>**0.61**</u>	1.0																	
Or	<u>**0.54**</u>	**0.42**	1.0																
Of	<u>**0.70**</u>	<u>**0.59**</u>	<u>**0.77**</u>	1.0															
Ep	0.25	<u>**0.62**</u>	**0.44**	**0.38**	1.0														
On	0.25	<u>**0.56**</u>	0.02	0.14	***0.30***	1.0													
Ef	<u>**0.69**</u>	<u>**0.59**</u>	<u>**0.55**</u>	<u>**0.77**</u>	0.28	0.18	1.0												
Ce	***0.29***	0.19	<u>**0.74**</u>	<u>**0.61**</u>	0.20	0.0	**0.39**	1.0											
Oo	0.05	-0.08	<u>**0.48**</u>	0.27	0.17	0.18	0.09	<u>**0.65**</u>	1.0										
Ov	0.0	0.16	***0.30***	0.16	0.24	0.1	0.13	<u>**0.51**</u>	***0.33***	1.0									
tot.t	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.0								
Ai	-0.11	***-0.31***	-0.15	***-0.31***	-0.22	-0.03	***-0.29***	-0.18	-0.01	-0.09	-0.25	1.0							
Bg	0.0	-0.02	0.16	-0.03	-0.18	-0.07	0.19	0.16	0.11	0.19	0.03	0.06	1.0						
Ss	-<u>**0.49**</u>	**-0.39**	-0.2	-0.27	-0.18	***-0.31***	-0.23	-0.10	-0.13	0.03	**-0.43**	-0.04	-0.03	1.0					
Pv	-0.17	0.23	-0.18	-0.20	***0.35***	**0.41**	-0.16	-0.12	-0.11	0.26	-0.03	0.23	-0.12	0.07	1.0				
Em	0.0	0.17	-0.05	-0.16	-0.02	-0.12	-0.11	-0.10	0.01	-0.18	-0.11	***0.35***	**0.43**	-0.13	-0.17	1.0			
Ll	-0.02	0.12	0.01	-0.11	***0.35***	**0.39**	-0.11	-0.14	0.17	-0.13	0.05	0.20	0.06	-0.11	**0.37**	0.03	1.0		
Oh	-0.03	0.13	0.28	0.13	***0.32***	-0.06	0.17	0.17	-0.08	0.02	0.14	0.21	-0.04	0.27	**0.37**	-0.15	0.17	1.0	
tot.d	-<u>**0.49**</u>	***-0.31***	-0.13	-0.26	-0.04	-0.23	-0.20	-0.08	-0.13	0.04	***-0.36***	NA	NA	NA	NA	NA	NA	NA	1.0

Significance levels: P < 0.05 at r = 0.29 (bold and italicised); P < 0.01 at r = 0.37 (bold); P < 0.001 at r = 0.46 (bold and underlined)

Cs = *Caccobius schreberi* (L.), Ef = *Euoniticellus fulvus* (Goeze), Ep = *Euoniticellus pallipes* (Fabricius), Of = *Onthophagus furcatus* (Fabricius), On = *Onthophagus nuchicornis* (L.), Oo = *Onthophagus opacicollis* Reitter, Or = *Onthophagus ruficapillus* Brullé, Ot = *Onthophagus taurus* (Schreber), Ov = *Onthophagus vacca* (L.) (Scarabaeinae); Ai = *Acanthobodilus immundus* (Creutzer), Bi = *Bodiloides ictericus ssp. ghardimaouensis* Balthasar, Ce = *Colobopterus erraticus* (L.), Em = *Esymus merdarius* (Fabricius), Ll = *Labarrus lividus* (Olivier), Oh = *Otophorus haemorrhoidalis* (L.), Pv = *Planolinellus vittatus* (Say), Ss = *Subrinus sturmi* (Harold) (Aphodiinae); tot. = total; t = tunneller; d = dung dweller, NA = not applicable
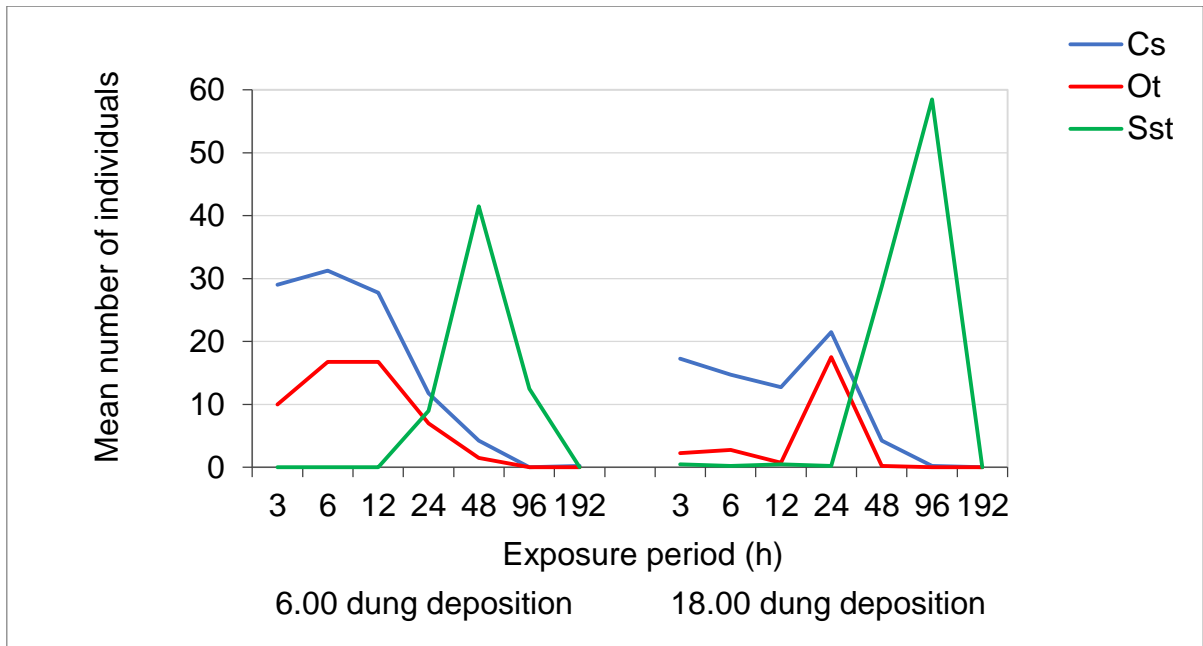
Figure 4.1 Mean number of individuals of the most common tunnelling dung beetles, *Caccobius schreberi* (Cs) and *Onthophagus taurus* (Ot), and the most common dung dweller, *Subrinus sturmi* (Sst), in standardised dung pads in the Kizilirmak Delta on the Black Sea coast of Turkey
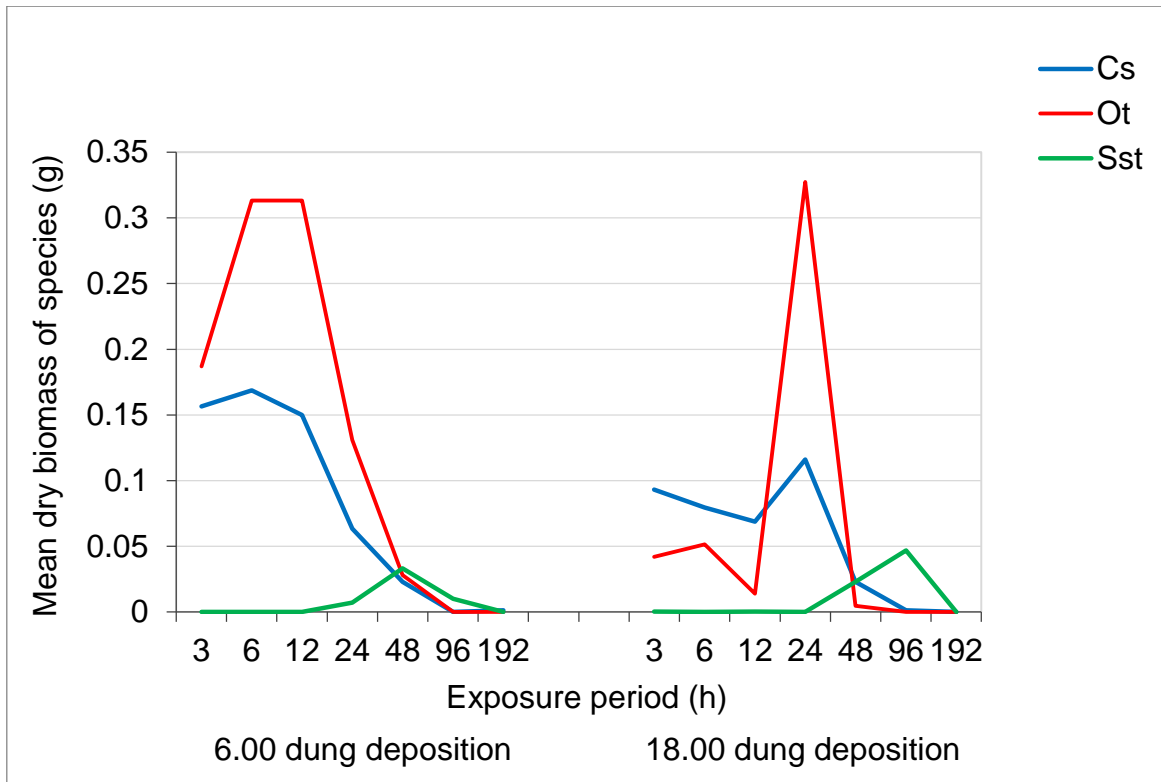
Figure 4.2 Mean dry biomass of the most common tunnelling dung beetles, *Caccobius schreberi* (Cs) and *Onthophagus taurus* (Ot), and the most common dung dweller, *Subrinus sturmi* (Sst), in standardised dung pads in the Kizilirmak Delta on the Black Sea coast of Turkey

A. 6.00 dung deposition time

$y = 0.0087x^3 - 0.164x^2 + 1.0306x + 0.0526$

$R^2 = 0.8116$

$r^2 = 0.868$

$P < 0.01$

B. 18.00 dung deposition time

$y = 0.0073x^3 - 0.111x^2 + 0.6979x + 0.1433$

$R^2 = 0.674$

$r^2 = 0.799$

$P < 0.01$
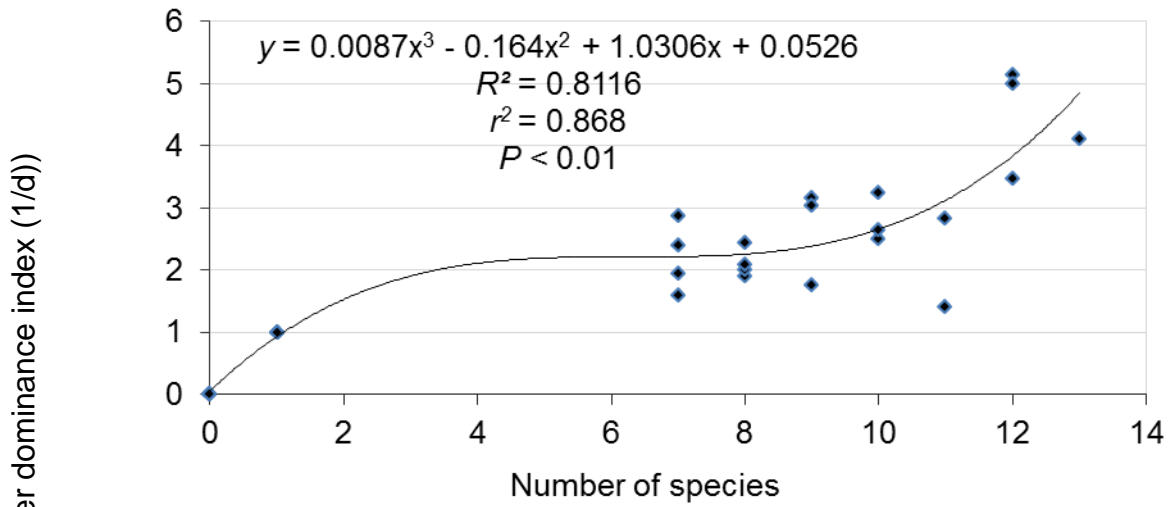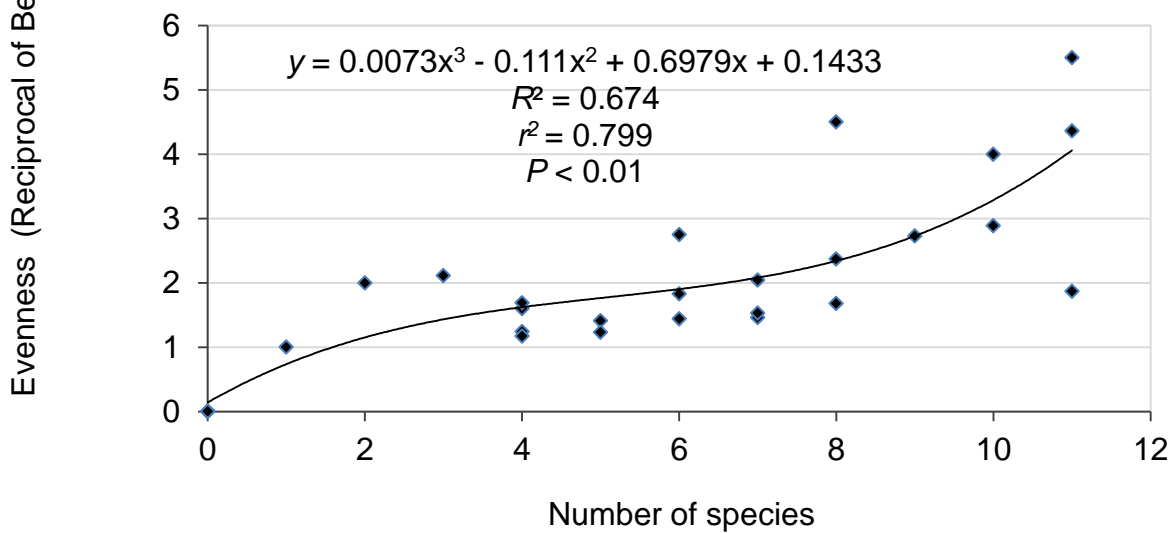
Figure 4.3 A, B Fitted regression curves for the relationship between the number of dung beetle species and their evenness of abundance (inverse of the Berger-Parker dominance index (1/d)) in standardised dung pads in the Kizilirmak Delta on the Black Sea coast of Turkey

CHAPTER 5   Temporal resource partitioning and interspecific correlations in a warm, temperate climate assemblage of dung beetles (Coleoptera: Scarabaeidae)

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5.1 Abstract

Guilds of dung dwelling and tunnelling dung beetles coexist in local assemblages in warm temperate regions, despite the tendency of dwellers to be inferior competitors. A field experiment on the Black Sea coast of Turkey examined the role of temporal separation and temporal resource partitioning in their coexistence. Standardised dung pads deposited at 4 h intervals through a 24 h period in summer were collected 12, 24 or 48 h later. Adults from 10 tunnelling and seven dung dwelling species were identified. The tunnellers contributed a high proportion of both total abundance and biomass. There were significant effects of both dung deposition time and exposure period on mean tunneller abundance. Mean tunneller abundance was nearly seven times higher in dung deposited at 06:00 than at 18:00. The dwellers reduced the potential for competitive interactions with tunnellers by relatively uniform dispersal across the six dung deposition times. The distinctly different dung use patterns by dwellers and tunnellers demonstrated temporal separation and by inference, temporal resource partitioning. Interspecific correlation coefficients were also determined because interspecific relationships are at the core of resource partitioning.

Total tunneller and dweller abundances were not correlated. Overall, there were strong, positive correlations between tunnelling species, low correlations between tunnelling and dwelling species and low correlations between dwelling species. The five most abundant tunnellers, from two tribes and three genera, were strongly, positively correlated. There were substantial size differences among the four most abundant tunnellers that may facilitate their coexistence.

Key words: coexistence, dung beetle, interspecies aggregation, Kizilirmak Delta, resource partitioning

5.2 Introduction

Nichols et al. (2008) reported in a review that dung beetles perform ecological functions and provide ecosystem services in natural environments and agroecosystems in temperate, subtropical and tropical environments by increasing the rates of dung degradation and nutrient cycling, dispersing seeds and reducing levels of pests that afflict humans and animals. The four dung beetle guilds, or functional groups, utilize contrasting nesting strategies; tunnellers construct brood balls in tunnels under or close to dung pads, dung dwellers brood in the dung pad or at the soil–dung interface, ball rollers bury their dung balls away from the pad, and kleptocoprids use dung separated from the dung pad by ball rollers and tunnellers (Doube 1990, Hanski and Cambefort 1991c, Krell et al. 2003). Dung dwelling species predominate in cool, temperate regions of the northern hemisphere (Hanski and Cambefort 1991c, Hutton and Giller 2004). The number of species of dwellers does not change substantially with decreasing latitude but their relative abundance is reduced by competition with the larger rollers and tunnellers (Hanski and Cambefort 1991c) which tend to be superior competitors (Doube 1990).

How are dung dwelling species able to persist in environments where they are potentially outcompeted and excluded? Mechanisms that contribute to the coexistence of competitors are aggregated spatial distribution (Ives 1988, 1991; Hartley and Shorrocks 2002) and spatial and temporal resource partitioning (Krell et al. 2003, Krell-Westerwalbesloh et al. 2004). In addition, the local community may be stable because it is below the level of saturation, the point at which it becomes unstable and species can be excluded (Horgan 2006). Ives (1991) and Hartley and Shorrocks (2002) reported that intraspecific and interspecific aggregation reduce interspecific competition when intraspecific aggregation is

higher. The 'aggregation model of coexistence' (Hartley and Shorrocks 2002) proposed that when individuals of a single species are concentrated together they inhibit their own population growth more than they inhibit other species, and that even when species use the same type of resource, their coexistence is facilitated where the distribution of individuals varies across patches. Dung beetle aggregation has been studied in cool temperate (Hutton and Giller 2004), subtropical (Giller and Doube 1994) and tropical (Horgan 2006) environments. Hanski (1991b) reported that pairwise interspecific aggregation (covariance) increases with the increasing ecological and morphological similarity of species.

Spatial and temporal (seasonal) resource partitioning have been reported from warm temperate areas (Jay-Robert et al. 2008). Factors that contribute to temporal resource partitioning by dung beetles at the species and guild levels include the age of dung (Palestrini et al. 1998), time of day of dung deposition (Krell-Westerwalbesloh et al. 2004), seasonality (Montes de Oca and Halffter 1995, Jay-Robert et al. 2008) and diel activity (Boonrotpong et al. 2012). Schoener (1986) reported that temporal resource partitioning is less common than spatial separation and trophic specialization but Krell-Westerwalbesloh et al. (2004) reported that temporal resource partitioning is a widespread mechanism that reduces competition.

The Kizilirmak Delta on the Black Sea coast of northern Turkey experiences a warm, temperate climate. Twelve dwelling, ten tunnelling and one large ball rolling species have been reported from the Kizilirmak Delta (Sullivan et al. 2016a). Assuming that the majority of the dwelling species have permanent breeding populations in the area, the question arises as to what mechanisms underpin their persistence in the face of potential competition from a large ball rolling species and tunnelling species. Is temporal resource partitioning one of the mechanisms? Therefore, the working hypothesis tested in this study in the Kizilirmak Delta was, 'There is a difference between the dung dwelling and tunnelling guilds in the temporal patterns of their use of dung'. That question was addressed by varying the time of deposition and the exposure period of standardised dung pads to determine whether they affect the mean abundance of the dwelling and tunnelling species. In addition, correlation analysis was used to determine the strength of interspecific relationships and their overall pattern.

5.3 Materials and methods

5.3.1 Study site

The experiment was conducted in the Kizilirmak Delta of Samsun Province on the Black Sea coast of Turkey. Free-ranging wild horses and domesticated cattle and sheep graze the extensive coastal dune system all year round and domesticated water buffalo are generally present from mid-April to mid-October. Large numbers of dung pads of all ages were distributed patchily around the study site before the experiment was established. The ridge line of the dune on which the experiment was conducted was sparsely covered with low, herbaceous vegetation, predominantly *Euphorbia terracina* L. Sullivan et al. (2016a) reported that the soil at the same site was essentially sand containing a small amount of organic matter.

5.3.2 Experimental conditions and design

Sunrise and sunset were at 05:28 hours and 19:53 hours on 31 July, 2015. Approximately 70 kg of very fresh water buffalo dung was collected from near an overnight camp of approximately 200 animals before 05:00 on that date. The dung was carefully screened for infestation by dung beetles, with none detected, before it was bulked, homogenized and chilled to 4 °C until used. A randomized complete block design was employed in the experiment. The sand was dry and relatively loose in the top 10 - 15 cm but moist and firmly packed below. Before deposition, the site for each pad was levelled by hand so that the pads were relatively flush with the sand surface. Standardised 1 kg pads (Rougon and Rougon 1991, Krell 2007) were formed in a plastic mould and deposited directly on the surface at 06:00, 10:00, 14:00, 18:00 and 22:00 on 31 July, 2015 and at 02:00 on 01 Aug., 2015, for collection 12, 24 or 48 h later. Eighteen pads, representing each of the six deposition times and three exposure period combinations, were randomly allocated to each of the four replicates (6 x 3 x 4 pads = 72 pads in total). The four replicates were arranged in two rows that each contained two replicates, with 10 m between the rows. Within each row, there was 6m between the replicates and within each replicate there was 5 m between pads (Sullivan et al. 2016 b). The length of each replicate was 85 m and the length of each row was 176 m.

During the experiment, the minimum and maximum temperatures ranged from 16 °C to 19 °C, and from 27 °C to 31.0 °C, respectively, at 1 m above ground level in the shade.

Eighteen millimeters of rain fell on the site between 06:00 hours and 07:00 on 2 August, 2015.

5.3.3 Dung pad collection and separation of dung beetles

At the three collection times, each pad and 10 cm of sand under the pad were collected. The sand was collected to capture individuals, especially tunnellers that escaped from the pad when it was disturbed during its collection. Dung fauna was collected from the dung pad and sand by flotation in water and then the sifting of the fibrous material and sand for missed specimens (Sullivan et al. 2016a). All specimens were preserved in 96% alcohol prior to identification. The ball roller, *S. sacer* L., which was active at some of the dung pads during the course of the experiment but not at the specific dung collection times, was the subject of a separate study (Sullivan et al. 2016b).

5.3.4 Identification

The dung beetles were identified by the first author (G. T. S.), with the aid of a Leica stereomicroscope (40X) and the Scarabaeoidea key of Baraud (1992), with the exception of *Euheptaulacus carinatus* (Germar), *Nialus varians* (Duftschmid) and *Pleurophorus* sp., which were identified by the fourth author (J.-P. L.). The single specimen of *Pleurophorus* sp. was damaged and unable to be identified to the level of species. Voucher specimens of all species collected are held at the Plant Protection Department, Faculty of Agriculture, Ondokuz Mayis University in Samsun, Turkey.

5.3.5 Dry weight (biomass) determination

The dry weight/biomass of individual species was calculated with a modified version of the methodology of Doube (1990). Thirty randomly selected individuals of each species, with the exception of *Labarrus lividus* (Olivier) (20 individuals), were oven dried for 24 h at 70° C. Following drying, the bulked individuals of each species were weighed on Precisa XB 629M scales sensitive to 0.001g. The mean dry weight per individual of each species was calculated by dividing the total dry weight of the individuals by the number of individuals.

5.3.6 Statistical analysis

To determine whether temporal separation and temporal resource partitioning had occurred, two-way ANOVA was used to examine the effects of dung deposition time and exposure period on mean dweller and tunneller abundance, after the data had been

transformed to make the variance independent of the mean, and the adjusted LSD test was used for the comparison of treatment means. As a measure of interspecific aggregation, the correlation coefficients of pairs of species across the six dung deposition times and three dung collection times were determined. ANOVA and interspecific correlations were done with the aov and cor functions of R-3.3.0 (R Development Core Team 2013), respectively. Analyses were limited to dwellers and tunnellers because on most occasions the activity of the ball roller *S. sacer* did not coincide with the collection times of the dung pads.

5.4 Results and discussion

5.4.1 Species, abundance and biomass

In this study from the central Black Sea coast of Turkey, 6,669 adult dung dwelling and tunnelling dung beetles, from 10 tunnelling species in four genera and seven dung dwelling species in seven genera, were collected (Table 5.1). Two species, *Euheptaulacus carinatus* and *Pleurophorus* sp., which were not reported by Sullivan et al. (2016a), were collected in the present study. The tunnellers contributed 89% of all individuals and 98% of total biomass; *Onthophagus taurus* (Schreber), *Onthophagus furcatus* (F.), *Caccobius schreberi* (L.) and *Euoniticellus pallipes* (F.) contributed 34%, 24%, 17% and 10% of abundance, respectively, and 63%, 9%, 9% and 12% of dry biomass, respectively. Similarly, from a seasonal study at two sites at different altitudes in southern France, Jay-Robert et al. (2008) reported that during spring/summer, small tunnellers regularly and strongly dominate abundance in dung beetle assemblages.

5.4.2 Dry biomass of dung pads and dung beetles

In the present study, the total wet weight of the original 72 dung pads was 72.0 kg and their total dry weight was 11.8 kg (16.4%). The total dry weight of the tunnellers and dwellers collected was 67.4 g (Table 5.1), which was 0.6% of the total dry weight of the original dung.

5.4.3 Effects of dung deposition time and exposure period

In the present study, the deposition of dung pads at four hour intervals over a 24 h period in midsummer and their collection 12, 24 or 48 h later revealed markedly different temporal

patterns of dung utilization by the dwelling and tunnelling guilds. Dung deposition time and dung age/exposure period were significant for mean tunneller abundance but without interaction; i.e., they were independent (deposition time: $F = 8.71$; $df = 5, 64$; $P < 0.001$; exposure period: $F = 5.95$; $df = 2, 64$; $P < 0.01$), and for mean dweller abundance, neither factor was significant (deposition time: $F = 1.71$; $df = 5, 64$; NS; exposure period: $F = 1.56$; $df = 2, 64$; NS) (Table 5.2). Mean tunneller abundance was highest at 24 h and lowest at 48 h ($P < 0.01$) across the six dung deposition times and higher in dung deposited at 06:00 than at 18.00 hours ($P < 0.001$) across the three exposure periods, with the differences in mean dweller abundance non-significant for the same analyses.

Mean tunneller abundance for dung pads deposited at 06:00 and 18:00 was approximately 21 and 2.5 times higher, respectively, than mean dweller abundance (Table 5.2). The dwellers dispersed much more uniformly across the six dung deposition times and three exposure periods than the tunnellers (Table 5.2), which meant they were able to occupy dung pads less densely populated with tunnellers, thereby reducing the potential for competition. These results reflect overall differences in the diel activity of tunnellers and dwellers and in the age of dung they are able to utilise. Furthermore, Lumaret and Kirk (1987) reported that i) tunnellers and dwellers are generally spatially separated within the same dung pad in zones with different moisture content, which reduces interguild competition; ii) individual tunnelling species nest at different depths, reducing intraguild competition; and iii) dwellers of the same size may not be active at the same time, thereby reducing intraguild competition.

5.4.4 Comparison of 2014 and 2015 data

The study of Sullivan et al. (2017b) (see Chapter 4) in mid-June, 2014, which was conducted at the same site as the current study, helps provide a broader perspective. The 2014 study had two of the same dung deposition times (06:00 and 18:00) and three of the same exposure periods (12, 24 and 48 h). The 24 equivalent dung pads from the 2014 and 2015 studies yielded 1,655 and 2,932 specimens, respectively. That meant that total abundance in early August (late summer) was 77% higher than in mid-June (early summer), albeit in different years. If these abundances are indicative of the within year and long term pattern, they would be in strong contrast to the low abundance reported by Lumaret and Kirk (1991) during the summer drought period in the Mediterranean region, possibly reflecting the less pronounced summer drought on Turkey's Black Sea coast.

In the 2014 study of Sullivan et al. (2017b), the five most abundant species for the 06:00 dung deposition, in descending order of abundance, were *Subrinus sturmi* (Harold), *C. schreberi, O. taurus, Onthophagus ruficapillus* Brullé and *Otophorus haemorrhoidalis* (L.). In 2015, for the same deposition time, the descending order of abundance was *O. furcatus, O. taurus, C. schreberi, E. pallipes* and *L. lividus.*

In June 2014 and August 2015, the total numbers of *O. furcatus* were 90 and 1,128, of *O. taurus* 101 and 554, of *C. schreberi* 175 and 459*,* and of *S. sturmi* 202 and 46*,* respectively. Substantial changes in the suite of species and their abundances in a short period were reported by Lumaret and Stiernet (1991) and Jay-Robert et al. (2008).

5.4.5 Spatial correlation of dwelling and tunnelling species

In the second component of the current study, the degree of association/aggregation of the commonest species was quantitatively investigated with correlation analysis. Specifically, interspecific (pairwise) correlation coefficients (Hanski 1991b) were determined for the 11 most abundant species, namely seven tunnellers from three genera and four dwellers from four genera, across the six dung deposition times and three dung collection times (Table 3). The remaining six species, *Colobopterus erraticus* (L.), *Onthophagus opacicollis* Reitter, *Onthophagus vacca* (L.), *E. carinatus*, *N. varians* and *Pleurophorus* sp., contributed 14 individuals in total and were excluded from the correlation analysis due to their low mean abundance (< 0.1 / pad).

In the current study, total tunneller and dweller abundances were not significantly correlated. However, the five most abundant tunnellers in descending order, *O. taurus*, *O. furcatus* and *C. schreberi* (Onthophagini), and *E. pallipes* and *Euoniticellus fulvus* (Goeze) (Oniticellini), were all positively and significantly correlated, with seven of the 10 correlations greater than r = 0.38 (P < 0.001) (Table 5.3). *Onthophagus taurus,* which was the largest and most abundant tunneller, contributed 34% of all individuals and 63% of total biomass. It was also highly, positively correlated with the next four most abundant tunnellers (P < 0.001). Overall, the highest correlation was between *O. furcatus* and *C. schreberi* (r = 0.81; P < 0.001) (Table 3). Hanski (1991b) reported that strong, positive correlations are indicative of similar ecology and morphology. At a more fundamental level, Ives (1988) reported that increasing spatial correlation between two species increases competition between them but intraspecific aggregation reduces the level of that competition and facilitates coexistence.

5.4.6 Size of tunnelling species and interspecific correlation

Lumaret et al. (1992) reported that abundant species in the same guild are able to coexist in dung because they are in different size classes. In the present study, the four most abundant tunnelling species (Table 5.1) contributed 85% of all dung beetles collected and 93% of the dry biomass. In descending order of abundance, the four species belonged to the size classes 5 (17 - 32 mg), 2 (3 - 4 mg), 3 (5 - 8 mg) and 4 (9 - 16 mg) of Lumaret et al. (1992). The fifth most abundant tunneller was in class 4 but it represented only 3% of total abundance and 5% of total dry biomass. The least abundant tunnellers, *Onthophagus nuchicornis* (L.) (class 3; Lumaret et al. 1992) and *O. ruficapillus* (class 2; Lumaret et al. 1992), were highly and positively correlated ($r = 0.72$; $P < 0.001$) but their correlations with the other five tunnellers were lower and variable, and particularly low with *O. taurus* (Table 5.3).

The question arises as to the reason for the generally high, positive correlations among tunnelling species, especially among the four most abundant species which were in different size classes. This pattern of interspecific aggregation may contribute to their coexistence through the collective changes they cause in the dung pad, including aeration and disintegration of its structure, during the excavation of dung.

5.4.7 Correlations of dung dwelling species

In the present study, the dwellers *L. lividus* and *Acanthobodilus immundus* (Creutzer) were positively correlated ($r = 0.27$; $P < 0.05$) but both were negatively correlated with all tunnellers. *Otophorus haemorrhoidalis* was atypical in that it was significantly, positively correlated with five of the seven tunnellers, and significantly, negatively correlated with *A. immundus* ($r = - 0.30$; $P < 0.05$) (Table 5.3). In contrast, *S. sturmi* was not significantly correlated with any species, with most individuals collected when the activity of tunnellers and other dwellers had sharply declined.

From north temperate environments, Hanski (1986) reported that nine species of *Aphodius* (Aphodiinae) in natural dung had mostly non-significant correlations and Hutton and Giller (2004) reported negligible association for nine species of *Aphodius* in standardised dung pads in Ireland. In contrast, Holter (1982) reported positive associations for *Aphodius* species in standardised dung pads in Denmark, and from an alpine area in Italy, Palestrini

et al. (1998) reported that Aphodiinae species tended to aggregate and associate positively with *Onthophagus fracticornis* (Preyssler).

5.4.8 Co-occurrence of dung dwelling and tunnelling species

The aggregation of an individual species increases intraspecific competition relative to interspecific competition and results in a greater number of less densely populated or vacant sites in which less competitive species can breed (Giller and Doube 1994). Shorrocks and Rosewell (1987) and Krell-Westerwalbesloh et al. (2004) referred to these lower density sites as 'probability refuges' and 'temporal refuges', respectively. In the present study, the high, temporal variability of mean tunneller abundance (Table 5.2) would have made temporal refuges available to the dwelling species, which tend to be inferior competitors, thereby increasing their relative competitiveness and breeding opportunities. Furthermore, Hanski and Cambefort (1991a) reported that the relatively small size and high fecundity of inferior competitors helps them avoid exclusion from the local species pool, even at high levels of competition.

5.4.9 Concluding remarks

The present study demonstrated markedly different temporal dung use patterns by most species of both the dung dwelling guild as a group and tunnelling species as a group across six dung deposition times and three exposure periods that are indicative of temporal resource partitioning. Correlation analysis revealed the pattern of interspecific relationships underpinning that partitioning, with the tunnelling species showing a strong tendency to positively associate, and the dwelling species tending to avoid both the tunnelling species and other dwelling species, except in one case (Table 5.3). The current study was designed to examine interspecific and interguild relationships temporally, rather than determine whether intraspecific and interspecific aggregation patterns were actually reducing competition and facilitating coexistence, as did the studies of Hutton and Giller (2004) and Horgan (2006). The investigation of interscale movement (Horgan 2006) would also contribute to a more comprehensive understanding of the mechanisms facilitating co-occurrence or coexistence and supporting the maintenance of dung beetle diversity in the Kizilirmak Delta of Turkey and in warm, temperate climate dung beetle assemblages generally.

5.5 Acknowledgements

Table 5.1 Abundance and biomass of dwelling and tunnelling species in standardised dung pads in a summer assemblage of dung beetles in the Kizilirmak Delta in Samsun Province, Turkey

Species*	Number of individuals	Mean dry weight / individual (g)	Total dry weight (g)
Onthophagus taurus (Schreber)	2,279	0.0187	42.6
Onthophagus furcatus (F.)	1,633	0.0038	6.2
Caccobius schreberi (L.)	1,149	0.0054	6.2
Euoniticellus pallipes (F.)	630	0.0123	7.7
Euoniticellus fulvus (Goeze)	217	0.0153	3.3
Onthophagus ruficapillus Brullé	26	0.0044	0.1
Onthophagus nuchicornis (L.)	17	0.0077	0.1
Subtotal – tunnellers	5,951	-	66.2
Labarrus lividus (Olivier)	249	0.0017	0.4
Subrinus sturmi (Harold)	206	0.0008	0.2
Otophorus haemorrhoidalis (L.)	164	0.0027	0.4
Acanthobodilus immundus (Creutzer)	85	0.0038	0.3
Subtotal – dwellers	704	-	1.3
Total	6,655	-	67.5

*Species with mean abundance < 0.2/pad are not included in the table; tunnellers: *Colobopterus erraticus* (L.), *Onthophagus opacicollis* Reitter, *Onthophagus vacca* (L.); dwellers: *Euheptaulacus carinatus* (Germar), *Nialus varians* (Duftschmid) and *Pleurophorus* sp.

Table 5.2 Mean abundance (± SE) of two guilds of dung beetles in standardised dung pads in summer in the Kizilirmak Delta in Samsun Province, Turkey

Dung deposition time	Tunnellers	Dwellers
06:00	185 ± 43a*	9 ± 2a
10:00	71 ± 12b	11 ± 2a
14:00	66 ± 10b	13 ± 2a
18:00	27 ± 8c	11 ± 4a
22:00	77 ± 10b	7 ± 2a
02:00	76 ± 10b	6 ± 1a
Dung exposure period (h)	Tunnellers	Dwellers
12	92 ± 21ab	7 ± 1a
24	104 ± 19a	11 ± 2a
48	56 ± 9b	10 ± 1a

*In each sub-table, means followed by the same letter in the same column are not significantly different (Tukey's HSD, $P < 0.05$). Means are on the untransformed scale but significance is from the transformed analyses. For the tunnellers, deposition time and exposure period are independent

Table 5.3 Correlation coefficients for dwelling and tunnelling species in standardised dung pads in a summer assemblage of dung beetles in the Kizilirmak Delta in Samsun Province, Turkey

	Ot	Of	Cs	Ep	Ef	tot.5t	On	Or	tot.7t	Ll	Ss	Oh	Ai	tot.4d
Ot	Ot													
Of	**<u>0.57</u>**	Of												
Cs	**0.62**	**<u>0.81</u>**	Cs											
Ep	**<u>0.45</u>**	**0.36**	*0.26*	Ep										
Ef	**<u>0.40</u>**	*0.28*	**<u>0.41</u>**	**<u>0.66</u>**	Ef									
tot.5t	NA	NA	NA	NA	NA	tot.5t								
On	-0.05	0.01	*0.24*	-0.05	**0.33**	0.06	On							
Or	0.05	*0.25*	**0.37**	0.15	**0.33**	*0.27*	**<u>0.72</u>**	Or						
tot.7t	NA	NA	NA	NA	NA	NA	NA	NA	tot.7t					
Ll	-0.16	-0.11	-0.20	-0.18	-0.20	-0.18	-0.02	-0.07	-0.18	Ll				
Ss	0.03	-0.01	-0.10	0.18	-0.05	0.00	-0.04	-0.01	0.00	0.13	Ss			
Oh	0.15	*0.27*	*0.24*	**0.33**	**<u>0.59</u>**	**0.32**	*0.24*	0.18	**0.33**	-0.21	-0.11	Oh		
Ai	-0.11	*-0.23*	-0.10	-0.19	-0.16	-0.21	-0.07	-0.19	-0.22	*0.27*	0.22	**-0.30**	Ai	
tot.4d	-0.07	-0.02	-0.12	0.04	0.03	-0.05	0.05	-0.02	-0.04	NA	NA	NA	NA	tot.4d

Significance levels: P < 0.05 at r = 0.23; P < 0.01 at r = 0.30; P < 0.001 at r = 0.38
P < 0.05 (italicized), P < 0.01 (bold), P < 0.001 (bold and underlined)

Species with a mean number ≥ 0.1 / pad were included in the table: 1. Aphodiinae (dwellers): Ai = *Acanthobodilus immundus*, Ll = *Labarrus lividus*, Oh = *Otophorus haemorrhoidalis*, Ss = *Subrinus sturmi*; 2. Scarabaeinae (tunnellers): Cs = *Caccobius schreberi*, Ef = *Euoniticellus fulvus*, Ep = *Euoniticellus pallipes*, Of = *Onthophagus furcatus*, On = *Onthophagus nuchicornis*, Or = *Onthophagus ruficapillus*, Ot = *Onthophagus taurus*; tot. = total; t = tunneller; d = dweller, NA = not applicable

CHAPTER 6 Unpublished Research, Synthesis and Conclusions

6.1 Unpublished experiments, analyses and draft manuscript

6.1.1 Experiment 4

Preamble

The large dung ball roller*, Scarabaeus sacer* L., was excluded from standardised, homogenised, 1 kg water buffalo dung pads with wire mesh (see Plate 11) to investigate the effects on succession; the mesh size allowed easy access to all other species, namely dung dwellers and tunnellers, in the local assemblage. The experiment was conducted on the same site as experiments 1, 2 and 3 that were published as Chapters 3, 4 and 5, respectively.

Experimental period: 10-14 July, 2015

Experimental design: Mesh/No mesh x 1 dung deposition time (18.00) x 5 dung exposure periods (6, 12, 24, 48 and 96 h) x 4 replicates (very few *S. sacer* came to the pads during the first six hours so the 6 h collection time was changed to 36 h).

The working hypothesis tested was, '*S. sacer* affects the temporal abundance of both the dung dwelling and tunnelling guilds.'

Results and Discussion: Relatively low numbers of *S. sacer* were present during the course of the experiment, even with rainfall events that kept the dung from drying for longer periods. Generally, *S. sacer* individuals tended to aggregate (see Chapters 3-5), which meant that there were usually pads untouched or relatively untouched and therefore available for exploitation by the smaller species. Total numbers of dung beetles at each collection time for the mesh and no mesh treatments are shown in Table 6.1. Analysis of the data at the level of individual species would likely reveal 'exposure period' effects and may reveal mesh' effects and 'mesh x exposure period' interactions.

Plate 11 Exclusion of the large dung ball roller, *Scarabaeus sacer* L. with mesh from a standardized 1kg dung pad in the Kizilirmak Delta, Turkey

Table 6.1 Numbers of dung beetles following the exclusion or non-exclusion of *Scarabaeus sacer* L. from dung pads in the Kizilirmak Delta, Turkey

Dung exposure period (h)	Number of specimens (No mesh)	Number of specimens (Mesh)
12	191	152
24	300	360
36	474	452
48	477	364
96	203	321
Total	1,645	1,649

6.1.2 Experiment 5

Preamble

Exclusion mesh of different sizes was used to investigate the effects of the exclusion of dung beetle species of different sizes on the composition of the assemblage able to access the pads. The experiment was conducted on the same sand dune site in the Kizilirmak Delta as Experiments 1, 2 and 3 that were published as Chapters 3, 4 and 5, respectively, and Experiment 4, which is described in 6.1.1.

The site is representative of the areas frequented by *S. sacer*; they are only active on the almost bare areas because they are unable to bury their dung balls where there is matted grass or dense roots. These bare areas, which are like a series of islands dispersed across the coastal dunes, represent an estimated 20% of the total area of the dune system. Spatial replication of this experiment on the other 80% of the dunes would have meant that *S. sacer*, representing approximately 80% of the assemblage biomass in both Experiments 2 and 3 (see Chapters 4 and 5), was absent.

In addition, differences across sites in the sand moisture content, slope, aspect, shading by trees and shrubs and amount of wind exposure potentially confound any comparisons with the bare areas.

Furthermore, in areas with thick herbaceous vegetation or matted grass cover, i.e., the areas of the sand dunes where *S. sacer* is not found, it is virtually impossible to quickly retrieve dung pads and the soil immediately under them due to the presence of numerous, intertwining plant roots. That means that an unknown number of tunnelling dung beetles, possibly many, are likely to escape into the soil. That in turn means that results may considerably underrepresent the tunnelers in both abundance and biomass and also negatively impact on the accuracy of interspecific correlations.

Experimental design: Six different mesh sizes (2.5, 4, 5, 6, 8 and 10 meshes/2.5 cm^2) x 1 deposition time (6.00 am) x 1 exposure period (48 h) x 4 replicates; standardised, homogenised 1 kg water buffalo dung pads were employed as the experimental units.

The working hypothesis tested was, 'The exclusion of larger species from dung pads by using mesh affects the abundance of smaller species that are able to access the dung through the mesh.'

Experimental period: 31 July – 2 August, 2015

Summary of results and discussion: The results of this experiment have initially proved inconclusive because some species had a substantial size range that meant that not all specimens were excluded by a particular mesh size. A case in point was *Onthophagus taurus* (Schreber), the most common and highest biomass tunnelling species on the experiment site. However, analyses based on biomass comparison may prove useful. For example, if larger specimens (irrespective of species) are excluded from dung, are smaller specimens (irrespective of species) more common, less common or unaffected. Such information may point to whether the numbers of smaller specimens (and species) are limited by larger specimens (and species) and whether competition is occurring.

6.1.3 Analyses of Chapter 5 data for individual species

Preamble

For Experiment 3 (see Chapter 5) of the thesis, all analyses were conducted solely on the basis of guilds/functional groups.

Experimental design: Two dung deposition time (6.00, 18.00) x 5 dung exposure periods 3, 6, 12, 24, 48, 96 h and 192 h) x 4 replicates using standardised, homogenised 1 kg pads of water buffalo dung.

Experimental period: 15 - 23 June, 2014

Results and Discussion

Example analyses

1) *Onthophagus taurus* (Schreber), the highest biomass tunnelling species in the summer assemblage

Type 3 tests of fixed effects for *Onthophagus taurus*				
Effect	Num DF	Den DF	F Value	Pr > F
Dung deposition time	1	27.7	31.50	<.0001
Dung exposure period	6	27.7	28.30	<.0001
Time*Exposure	6	27.7	22.98	<.0001

2) *Subrinus sturmi* **(Harold),** the most common dung dwelling species in the summer assemblage

Type 3 tests of fixed effects for *Subrinus sturmi*				
Effect	Num DF	Den DF	F Value	Pr > F
Dung deposition time	1	38.4	0.06	0.8111
Dung exposure period	6	38.4	30.91	<.0001
Time*Exposure	6	38.4	5.23	0.0005

The same analytical procedures were adopted for the other 15 species collected in this study. Overall, the results indicate that the factors/variables shown to be significant at the guild/functional group level in Chapters 4 and 5, namely 'time of dung deposition', 'exposure period' and 'time x exposure', are also significant in various combinations at the species level. The data needs additional analysis and interpretation before publication.

6.1.4 Draft manuscript: Dung beetles (Coleoptera: Scarabaeidae), phylogenetic dispersion and theories of coexistence

Preamble

The following draft abstract, which was based on the data and analyses in Chapters 4 and 5 of this thesis, explores the potential of patterns of relatedness in two dung beetle assemblages to inform the debate on evolutionary theory. The draft manuscript, which can be seen in full as Appendix 2, requires considerable further development, including ecological modelling and the reinterpretation of data.

6.1.4.1 Abstract

Classical niche theory, the traditional competition-relatedness theory and modern coexistence theory all predict phylogenetic over-dispersion under many circumstances but the coexistence theory also allows for phylogenetic under-dispersion, i.e., the coexistence of closely related species. Dung beetles (Coleoptera: Scarabaeidae) live in multispecies communities associated with small, ephemeral, temporally and spatially dispersed units of animal dung. Results from two published field studies that investigated temporal changes in the mean abundances of tunnelling species (Scarabaeinae) and dung dwelling species (Aphodiinae) and their correlation patterns in standardized dung pads were used to make inferences about the contradiction between the theories. Mean numbers of dung dwelling species were much more uniform for dung deposition time and exposure period than the tunnelling species, thereby reducing potential interference competition by the tunnellers. Correlation analysis for all pairs of species generally showed very high, positive correlations between six tunnelling species in three genera of Scarabaeinae (most r values at P < 0.001); low correlations between tunnelling and dung dwelling species in nine genera of Aphodiinae; and low correlations between the dwelling species. The six highly correlated, closely related Scarabaeinae species across the two experiments, including three *Onthophagus* species and two *Euoniticellus* species, also collectively contributed a very high proportion of total dung beetle abundance. Diel activity patterns, and probably environmental filtering at the level of dung moisture content, resulted in temporal resource partitioning between the Aphodiinae and Scarabaeinae. These two phenomena operating in sequence appear to constitute the mechanisms driving community underdispersion or clustering at the study site. The generally very strong association of closely related species of Scarabaeinae and their much weaker association with species of Aphodiinae may

provide evidence that supports the contemporary coexistence theory's assertion that increasing phylogenetic proximity, or relatedness, does not necessarily cause competitive exclusion.

6.2 Overview of thesis, including unpublished material

Chapter 1 provides the background and rationale for this thesis which addressed various aspects of resource use by dung beetles (Coleoptera: Scarabaeidae; Aphodiinae, Scarabaeinae). A survey was conducted during 2013 to document the assemblages on two distinct, adjacent soil types in the Kizilirmak Delta on the central Black Sea coast of northern Turkey (see Chapter 2). That survey recorded 23 dung beetle species of three guilds, namely a ball roller, dung dwellers and tunnellers that had not previously been documented from the study area (Appendix 1). In addition, that survey showed that there was sufficient abundance of the three guilds to conduct three field experiments with standardised dung pads in 2014 (Chapters 3, 4) and 2015 (Chapter 5). That determination was crucial given that outside of the study area dung beetle richness and abundance have been greatly reduced by both a shift from open grazing to intensive husbandry in barns and the use of parasiticides that are toxic to dung beetles. The first experiment conducted in 2014 investigated the effects of dung pad size on aspects of dung ball production by *S. sacer*. A second experiment conducted in 2014 and a third in 2015 focused on the colonisation and succession of dung beetles in standardised dung pads from the time of dung deposition to the point of rejection as a food resource.

Specifically, the first experiment investigated aspects of the ecology of a dominant species, the large ball roller, *S. sacer*, with standardised dung pads across a 16-fold size range, namely 125 g to 2,000 g (Chapter 3). Dominant species can strongly influence community succession in pads so the experiment was designed to investigate ball production, specifically the effects of dung pad size on the number and size of balls produced, and in what period(s) during the 24 hr cycle the balls are produced. The other two field experiments (Chapters 4, 5) investigated community succession, particularly in the first 24 h, a largely neglected period. The first experiment was conducted in mid-June (early summer) of 2014 and the second was conducted in late July - early August (late summer) of 2015. Standardised dung pads formed from fresh, homogenised water buffalo dung were used in the series of three replicated plot field experiments because their size, shape and time of deposition and collection can be predetermined. Species and guild

richness, abundance and biomass were the parameters used to compare temporal changes in assemblage composition during succession and correlation analysis was employed to determine the patterns of interspecific, intraguild and interguild relationships involved.

Specifically, the experiments investigated how species, genera and guilds interact from 3 hours to 8 days after the deposition of standardised dung pads at different times in the 24 h cycle. These experiments yielded an additional 4 species (Appendix 1) not collected in the survey of 2013. Regression analysis demonstrated a highly significant relationship between species richness and the inverse of the Berger-Parker dominance index (d); i.e. the more species in any set of equivalent dung pads, the less likely it was that any particular species or small number of species would dominate in terms of abundance. Separately, ANOVA and correlation analysis were used to examine the temporal changes in guild abundance, and intraguild and interguild relationships, respectively. ANOVA showed a distinct pattern of temporal separation between species of the dung dwelling and tunnelling guilds, although there was some overlap. This temporal separation appears to have been attributable to differences in diel activity and different tolerance limits for abiotic factors, especially dung moisture content, which would be an example of habitat filtering. Correlation analysis generally showed very strong, positive correlations between tunnelling species, low correlations between tunnelling and dwelling species, and also low correlations between dwelling species. These phenomena collectively revealed the pattern of aggregation underpinning temporal separation and also temporal resource partitioning, assuming that presence in dung indicates use. Furthermore, some species were not present in one experiment or the other and the abundances of individual species varied widely. Correlations between the same species between 2014 and 2015 ranged from almost the same to considerably different. However, the same overall pattern of intraguild and interguild correlations was evident.

The temporal resource partitioning evidenced in the 2014 and 2015 experiments may reduce competition and contribute to the coexistence of the tunnelling and dung dwelling guilds with *S. sacer*, the dominant competitor, but that would need to be confirmed with additional field experiments. It is important to note that during the short, intense, peak ball production period of *S. sacer*, a considerable number of pads were only partially used and others were untouched. This means that over any 24 h period when *S. sacer* is active a high proportion of pads or portions of pads are available to sustain the tunnelling and

dwelling species. The tunnellers, because of their superior competitive ability, could potentially dominate this remaining resource but the behaviour of the dwellers in generally avoiding tunnellers and each other allows them to exploit zones of less densely populated dung termed 'temporal refuges' by Krell-Westerwalbesloh et al. (2004).

Experiments 4 and 5 (see Sections 6.1.1 and 6.2.2) attempted to build on the results of the earlier experiments by manipulating the dung environment through the use of mesh of various sizes to exclude different segments of the dung beetle assemblage. The aim was to determine i) the effects of exclusion of increasing numbers of species on the abundance and biomass of the species able to pass through the mesh and ii) the effects of their exclusion on the strength of interspecific correlations. Questions of interest include: Does the exclusion of larger species lead to increases in the abundance of smaller species and are the exclusions reflected in the changes in the correlations at the interspecific, intrageneric, intraguild and interguild level that were reported in the experiments described in Chapters 4 and 5? This information may shed light on whether competition and even facilitation are involved in shaping the assemblage. As stated in Sections 6.1.1 and 6.2.2, the data generated in these experiments needs considerable further analysis and interpretation before publication.

6.3 Contributions to ecological theory

This study demonstrated that temporal separation, and by inference, temporal resource partitioning, is occurring in a warm temperate climate assemblage of dung beetles. In conjunction, by employing correlation analysis, the study was able to determine the strength of the interspecies, intragenus, intergenus, intraguild and interguild relationships that underpin community function. That correlation analysis revealed that the overall pattern of the relationships between dwelling species, between tunnelling species, and between dwelling and tunnelling species, is quite similar at different times of the summer and between years at the same site.

Diel activity initially determined the subgroup of tunnelling species from the local species pool that could co-occur in a particular dung pad. Habitat filtering appears to have further restricted the number of species to those tolerant of the prevailing abiotic conditions in that pad, especially the moisture content. Niche partitioning based on size difference, referred to as 'limiting similarity', appears to have further restricted the number of species that could be both concurrent and abundant. The strong association of tunnelling species,

which probably reflected higher levels of negative intraspecific interactions than negative interspecific interactions, and similar competitive abilities, provided opportunities for the less competitive dwelling species to occupy temporal refuges.

The overall pattern of interspecific, intraguild and interguild correlations, which further evidenced temporal resource partitioning, may lend support to contemporary coexistence theory's contention that increasing phylogenetic proximity or relatedness does not necessarily lead to competitive exclusion. Overall, the experiments and analyses across this study showed that through temporal resource partitioning, representatives of the three major dung beetle guilds, namely a ball roller, dung dwelling species and tunnelling species, interact in a manner that reduces the potential for competition, to the advantage of the less competitive tunnelling species and the even less competitive dung dwelling species. For confirmation, this assertion would need to be examined in experiments specifically designed to test whether intraspecific competition is greater than interspecific competition.

6.4 Implications for management

The current study demonstrated the presence of a species-rich dung beetle community comprised of three guilds in the RAMSAR-listed Kizilirmak Delta of Turkey. Sustainable levels of grazing of the area by water buffalo, cattle, sheep and horses can continue to provide a diverse, year round dung resource for coprophilous insects. However, Verdú et al. (2018) reported that the use of parasiticides on livestock should be managed so as to minimize the risk of the poisoning of dung beetles and other coprophilous fauna by expelled residues in dung. The network of strong, positive correlations between tunnelling species may indicate that the collective functionality of that guild is vulnerable to loss of efficiency, or partial collapse, if one or more species are lost from the assemblage. The large, ball roller *S. sacer* is an iconic species and its presence can help raise the public profile of the Kizilirmak Delta and its conservation values. *Scarabaeus sacer* is particularly vulnerable to vehicular traffic. The installation of warning notices (Plate 12), the reduction of traffic flows and the slowing of traffic, especially during its peak activity period during late dusk and early night, should therefore be priorities. Off-road vehicular traffic should also be strictly regulated. This species may be also at risk from commercial collection so the appropriate management measures should be put in place to minimize that risk.

Plate 12 'Caution: dung ball rollers' sign – Coto Doñana National Park, Spain (photo courtesy of J-P Lumaret)

6.5 Approach and limitations

While dung beetles were the focus of this study, the experimental design could also be employed to better understand temporal changes in the populations of other coprophilous insects such as the Histeridae, Hydrophilidae and Staphylinidae, and the population dynamics in other ephemeral habitats such carrion, fruit and mushrooms, in which rapid succession occurs. A limitation of the study was the use of standardised pads that do not reflect the natural variability of the size and shape of dung pads. An additional limitation was the non-inclusion of the highest biomass species, the ball roller *S. sacer*, in ANOVA and correlation analyses because of its short activity period; the low probability of its occurrence at the dung pads at the designated collection times meant that it could have been grossly underrepresented in sampling, which would have compromised the accuracy of statistical analyses.

Temporal replications of the experiments across the seasons would have facilitated a better understanding of the mechanisms involved in temporal resource partitioning, and the factors contributing to it. Spatial replications of the succession experiments would have allowed the determination of the level of intraspecies competition relative to interspecies competition and hence the determination of whether coexistence is a factor shaping the composition of local assemblages, as distinct from species simply co-occurring. However, as explained in Sections 6.1.1 and 6.1.2, spatial replication would have been compromised by the loss of the highest biomass species, *S. sacer*, and also by the difficulty of collecting dung pads and the soil under them without the escape of many individuals, especially of the tunnelling species, because of the presence of dense matted grass and plant roots that make the rapid collection of dung pads and the soil under them very difficult.

6.6 Future research possibilities

More exclusion studies involving different sizes of mesh and assemblages of dung beetles in different environments, and also 'inoculation' studies with various core species and satellite species, especially *S. sacer* and *O. taurus*, would yield additional insights into the interrelationships between dung beetle species, genera and guilds. The questions 'to what extent' and 'why' correlation coefficients between the same species vary are worth pursuing. Is the phenomenon related to: abundance or biomass? the species mix? season? and/or dung deposition time and/or dung exposure period? Conducting a time of dung deposition x exposure period study in winter when dwelling species dominate species richness and abundance would like generate interesting additional insights into the patterns of association of species.

Separately, does the size of the dung pad affect temporal and spatial dung use patterns and interspecies correlations, and to what extent? In addition, the investigation of the actual levels of intraspecific and interspecific aggregation would establish whether the pattern of aggregation is facilitating coexistence; Ives (1991) and Hutton and Giller (2004) reported that if the level of intraspecific aggregation is greater than that of interspecific aggregation, coexistence is being facilitated.

Investigation of the specific reasons for the generally very strong, positive correlations between tunnelling species, despite the large amount of unused dung in the present study, would also contribute to a better understanding of niche partitioning, competition, facilitation and evolutionary relationships.

The contemporary coexistence theory (Mayfield and Levine 2010) promotes the role that relative fitness differences and stabilizing niche differences play in shaping interactions between species and their environment, both abiotic and biotic, during the assemblage of communities. The mechanisms by which relative fitness differences and stabilizing niche differences shape dung beetle communities would be a fertile area for further research. More broadly, the application of the contemporary coexistence theory to the intricate network of temporal and spatial relationships between dung beetles and between other components of the dung fauna such as fungivores, detritivores, parasites, parasitoids and predators, would likely yield many new ecological insights.

6.7 Closing remarks and conclusions

In the present study of a warm temperate climate assemblage of dung beetles, rapid dung dehydration accelerated the rate of temporal succession, as occurs in dry subtropical and tropical environments. However, a critical difference between those environments and the current study was the relatively low number of ball rollers present and the absence of large tunnellers which can rapidly reduce the volume of the dung pad. The ball roller *S. sacer* strongly dominates the biomass of the local assemblage (>80%) but its short activity period in the 24 h cycle means that there is still a large amount of the total dung resource available to other users. That situation provides a less competitive environment in which small and medium-sized tunnellers and dwellers are able to persist.

In this study, the significant effects of dung deposition time, dung exposure period and their interaction on mean dwelling and tunnelling guild abundances, and the correlation patterns between species, were indicative of temporal resource partitioning. Its occurrence is likely to have been attributable to a combination of factors that included intraguild and interguild differences in: diel activity; habitat filtering, most likely along the declining gradient of moisture content; intraguild and interguild patterns of association, as evidenced by correlation analysis; competitive ability differences; and size differences. Stabilizing mechanisms, which are essential for species coexistence, include resource partitioning, as well as mechanisms such as the 'storage effect', which depend on variations in population densities and environmental factors over space and time (Chesson 2000).

In the current study, correlation analysis revealed how temporal separation and temporal resource partitioning manifested in intraspecific and interspecific patterns of association that reduced the potential for interguild competition. Separately, it is possible that the

storage effect is also contributing to the co-occurrence, or possibly coexistence, of the three dung beetle guilds. As discussed in Section 6.5, additional temporal and spatial replications of the experiments conducted in this study would help to clarify which factors are involved in temporal and spatial resource partitioning, and the extent of their involvement, and whether the 'storage' effect is influencing community structure.

Furthermore, the generally strong, congeneric aggregation of the tunnelling *Onthophagus* spp. and *Euoniticellus* spp., lends tentative support to the contemporary coexistence theory's contention that increasing phylogenetic proximity or relatedness does not necessarily lead to competitive exclusion. However, this assertion requires additional experiments to be conducted for clarification. Separately, the network of strong, positive correlations between tunnelling species may indicate that the collective functionality of that guild is vulnerable to loss of efficiency if one or more species are lost.

Overall, the results of this study suggest that its methodology, supplemented by additional temporal and spatial field experiments, can provide deeper insights into the mechanisms underpinning the co-occurrence, and even the coexistence, of dung beetles, other dung fauna, fauna in other ephemeral resource patches, and insect faunas in general.

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Appendices

Appendix 1 Dung beetle (Scarabaeidae) species collected in the Kizilirmak Delta on the Black Sea coast of Turkey from 2013 to 2015

Subfamily	Species
Aphodiinae	*Acanthobodilus immundus* (Creutzer)*
	Aphodius fimetarius (L.)*
	Bodilus ictericus subsp. *ghardimaouensis* Balthasar*
	Bodilus lugens (Creutzer)*
	Chilothorax distinctus (Muller)*
	Colobopterus erraticus (L.)**
	Esymus merdarius (Fabricius)*
	Euheptaulacus carinatus (Germar)*
	Labarrus lividus (Olivier)*
	Melinopterus consputus (Creutzer)*
	Nialus varians (Duftschmidt)*
	Nimbus contaminatus (Herbst)*
	Otophorus haemorrhoidalis (L.)*
	Phalacronothus quadrimaculatus (L.) *
	Planolinellus vittatus (Say)*
	Subrinus sturmi (Harold)*
	Pleurophorus sp.*
Scarabaeinae	*Caccobius schreberi* (L.)**
	Euoniticellus fulvus (Goeze)**
	Euoniticellus pallipes (Fabricius)**
	Onthophagus furcatus (Fabricius)**
	Onthophagus nuchicornis L.**
	Onthophagus opacicollis Reitter**
	Onthophagus ruficapillus Brullé**
	Onthophagus taurus (Schreber)**
	Onthophagus vacca (L.)**
	Scarabaeus sacer L.***

*: dung dweller; **: tunneller; ***: ball roller

Appendix 2 Draft manuscript: Dung beetles (Coleoptera: Scarabaeidae), phylogenetic dispersion and theories of coexistence

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Abstract

Classical niche theory, the traditional competition-relatedness theory and modern coexistence theory all predict phylogenetic over-dispersion under many circumstances but the coexistence theory also allows for phylogenetic under-dispersion, i.e., the coexistence of closely related species. Dung beetles (Coleoptera: Scarabaeidae) live in multispecies communities associated with small, ephemeral, temporally and spatially dispersed units of animal dung. Results from two published field studies that investigated temporal changes in the mean abundances of tunnelling species (Scarabaeinae) and dung dwelling species (Aphodiinae) and correlation patterns in standardized dung pads were used to make inferences about the contradiction between the theories. Mean numbers of dung dwelling species were much more uniform for dung deposition time and exposure period than the tunnelling species, thereby reducing the potential for interference competition by the tunnellers. Correlation analysis for all pairs of species generally showed very high, positive correlations between six tunnelling species in three genera of Scarabaeinae (most r values at $P < 0.001$); low correlations between tunnelling and dung dwelling species in nine genera of Aphodiinae; and low correlations between the dwelling species. The six highly correlated, closely related Scarabaeinae species across the two experiments, including three *Onthophagus* species and two *Euoniticellus* species, also collectively contributed a very high proportion of total dung beetle abundance. Diel activity patterns, and probably environmental filtering at the level of dung moisture content, resulted in temporal resource partitioning between the Aphodiinae and Scarabaeinae. These two phenomena operating in sequence appear to constitute the mechanisms driving community underdispersion or clustering at the study site. The generally very strong association of closely related species of Scarabaeinae and their much weaker association with species of Aphodiinae provide tentative evidence that supports the contemporary coexistence theory's assertion that increasing phylogenetic proximity, or relatedness, does not necessarily cause competitive exclusion.

Introduction

The mechanisms involved in the assembly of communities and the coexistence of species have long occupied the thoughts of evolutionary biologists and ecologists (Mayfield and Levine 2010). The clarification of these mechanisms that influence the composition, diversity and relative abundance of co-occurring species in local communities is an urgent task because of the increasingly unsustainable levels of human impacts on the environment (Hobbs et al. 2009). According to the traditional competitiveness relatedness hypothesis, closely related taxa compete more intensely with each other than with more distantly related taxa, thereby limiting their ability to coexist (Webb et al. 2002). Species differences are involved in both enhancing coexistence through niche differences and limiting coexistence through competitive ability differences (Munkemuller et al. 2009).

Over the 15 year period to 2010, the role of competition in community assembly has increasingly been questioned, and in particular, modern coexistence theory, as applied to plants, has shown that trait similarity does not necessarily lead to competitive exclusion, as classically understood (Mayfield and Levine 2010). In addition, there is a growing appreciation that non-competitive processes, including facilitation (Valiente-Banuet and Verdu 2007) and demographic stochasticity (Hubbell 2001), may also play important roles in mediating patterns of relatedness in communities (Mayfield and Levine 2010).

A contemporary view of coexistence, involving both niche and competitive ability differences, predicts that the competition-relatedness hypothesis may prevail under certain circumstances, resulting in overdispersion (Maherali and Klironomos 2007; Jiang et al. 2010). In other situations, however, it is increasingly clear that competition can also result in relatedness patterns opposite to those expected under the competition-relatedness hypothesis, and specifically underdispersion, the coexistence of closely related species (Mayfield and Levine 2010). Each species in a community has an individual niche and competitive ability signature, but whether individual functional traits relate to one type of difference or another depends on the limiting factors for the community (Chesson 2000).

The coexistence of closely related species occurs when niche and fitness differences are small but niche differences are larger than fitness differences (Mayfield and Levine 2010).

This inequality of species differences is theorized to influence long-term stable coexistence, though others have noted that exclusion can be very slow, allowing for apparent coexistence over many years (Rydin and Barber 2001). In such cases, observed patterns may conflict with theoretical expectations.

The crucial difference between modern coexistence theory and the traditional competition-relatedness theory is that the former allows for the coexistence of closely related species (Mayfield and Levine 2010). Mayfield and Levine (2010) further stated that in plant communities, competitive exclusion can drive either phylogenetic over-dispersion or the opposite, underdispersion or clustering. Before that study, phylogenetic clustering was more widely believed to occur when environmental (habitat) filtering is stronger than competitive exclusion (Webb et al. 2002; Mayfield et al. 2005; Cavender-Bares et al. 2009). In contrast to ecological (niche) filtering, also known as species assortment, the concept of habitat filtering or environmental filtering (Cornwell et al. 2006) implies that species with similar ecological requirements should co-occur more often than expected. Clustering can result from environmental filtering; the difference now is that it is also accepted that it is possible to get the same patterns from competition (Cadotte and Tucker 2017; M. Mayfield, pers. comm. May, 2017).

Mayfield and Levine (2010) noted that there is growing consensus that coexistence in competitive plant communities is driven by the interaction of two types of differences between species, namely niche differences and competitive ability differences. Although this idea had become increasingly prominent over the previous five years, HilleRisLambers et al. (2012) noted that there is still a limited understanding of which niche axes and which traits determine the outcome of competition and community structure in plant communities.

The direct application of modern coexistence theory to the ecology of animals is relatively novel, making the subject of phylogenetic relationships and the causative mechanism(s) a potentially fertile area of both retrospective and new research.

Dung beetles (Coleoptera: Geotrupidae, Scarabeidae) utilise small, ephemeral, temporarily and spatially dispersed units of animal dung as a food and brooding resource. Guilds or functional groups of dung beetles use different nesting strategies; tunnellers construct brood balls in tunnels under dung pads, dung dwellers brood inside the dung pad or at the junction between soil and dung, ball rollers roll dung balls some distance from the pad before burial, and kleptocoprids use the dung removed from pads by ball rollers and

tunnellers (Doube 1990; Krell et al. 2003). Kadiri et al. (2014) reported that biological traits such as spatio-temporal reproductive patterns, different life histories and size of species play a major role in the co-existence of species in an assemblage. Simmons and Ridsdill-Smith (2011) reported that dung beetles have proved particularly useful for broad scale ecological studies that investigate fundamental issues in community and population ecology.

In this perspective paper, the results from two field experiments that investigated the interspecific and interguild relationships of dung beetles (Scarabaeidae: Aphodiinae, Scarabaeinae) were primarily used to attempt to clarify the contradiction between the classical niche and traditional competition-relatedness theories, and modern coexistence theory. Specifically, Sullivan et al. (2017a,b) investigated various aspects of dung beetle ecology, including temporal resource partitioning, on a coastal sand dune in the RAMSAR-listed Kizilirmak Delta in Samsun Province on the central Black Sea coast of Turkey in June, 2014 and August, 2015. These studies investigated short term changes in the species richness, abundance and biomass of dung beetles in standardized dung pads formed from homogenized water buffalo dung.

Methodology

For the purposes of the arguments presented and conclusions reached in this perspective, trait and niche differences collectively were assumed to be less between congeneric species than between non-congeneric species. In addition, the terms, 'tunnelling species' and 'Scarabaeinae', and 'dung dwellers' and 'Aphodiinae', are used interchangeably, despite there being exceptions. Four tables from Sullivan et al. (2017a,b) are included to facilitate understanding of the 'Discussion'. It should be noted that the experimental designs and analyses presented in the four tables were not specifically employed to analyse phylogenetic patterns. Other material from these two studies, and various insect studies, including dung beetle studies, were also used. They give the phylogenetic patterns of co-occurrence reported by Sullivan et al. (2017a,b) a broader ecological context for comparison of the abilities of the subject coexistence theories to explain these patterns.

Discussion

The subject of whether the aggregation patterns of closely related species support the modern interpretation of coexistence, or classical niche theory and the traditional competition relatedness theory, has been pursued with respect to plant communities but the potential contribution of animal communities to the debate has been largely neglected. The studies of dung beetle (Coleoptera: Scarabaeidae) assemblages by Sullivan et al. (2017a,b) in the Kizilirmak Delta in Turkey in 2014 and 2015, in conjunction with other dung beetles studies, have provided an opportunity to address that deficit.

Sullivan et al. (2017a) deployed standardized dung pads at four hour intervals over a 24 h period and collected them after three exposure periods, 12 h, 24 h and 48 h. The observed changes in the mean abundances of the tunnelling (Scarabaeinae) and dung dwelling (Aphodiinae) dung beetles over the 48 h period are shown in Table 1. Furthermore, they reported that in the course of temporal resource partitioning, there were generally strong, positive correlations between the tunnelling species, low correlations between tunnelling and dung dwelling species, and also low correlations between dung dwelling species (Table 2). The five most abundant, co-occurring species were tunnellers from three genera (*Caccobius*, *Euoniticellus* and *Onthophagus*) of two tribes of the subfamily Scarabaeinae. These species were all positively and significantly correlated with each other, with seven of the 10 correlations higher than r = 0.38 (P < 0.001).

In the second experiment, Sullivan et al. (2017b) employed two dung deposition times (6:00 and 18:00) and seven exposure periods from 3 h to 192 h to investigate different aspects of temporal resource partitioning (Table 3). In this study, the dwelling species again dispersed more uniformly than the tunnelling species along two of the three temporal axes (daily and succession) reported by Sladecek et al. (2017), thereby reducing the probability of competitive interactions with tunnelling species. As reported by Sullivan et al. (2017a), there were high correlations among the most abundant and closely related species. Five species from three genera (*Caccobius*, *Euoniticellus* and *Onthophagus*) of Scarabaeinae, including 3 *Onthophagus* species, were all positively and significantly correlated with each other, except in one case, with the other nine of ten correlations higher than r = 0.38 (P < 0.001) (Table 4).

Correlation analysis for all pairs of species of the two subfamilies across the two experiments reported by Sullivan et al. (2017a,b) generally showed very strong, positive

correlations between the most abundant tunnelling species in three genera of Scarabaeinae, with most r values at P < 0.001; low correlations between tunnelling species and dung dwelling species in nine genera of Aphodiinae; and low correlations between the dwelling species themselves. These phylogenetic patterns suggest a degree of underdispersion or clustering of species of the subfamily Scarabaeinae, including three *Onthophagus* species and two *Euoniticellus* species. This clustering is consistent with expectations, if there are higher levels of negative intraspecific interactions than negative interspecific interactions, and may indicate similar competitive abilities. The clustering is also consistent with the suggestion of Mayfield and Levine (2010) that closely related species of plants can coexist when niche and fitness differences are small and niche differences are collectively greater than fitness differences.

Across both the experiments of Sullivan et al. (2017 a,b), the generally much lower correlations of the Aphodiinae with the Scarabaeinae than the correlations among the Scarabaeinae themselves were attributable to both the more uniform colonisation of dung deposited at different times and the longer period of occupancy of pads by the Aphodiinae. Overall, the mean abundances of the Aphodiinae and Scarabaeinae and their patterns of interspecific correlations in the two field experiments reported by Sullivan et al. (2017a,b) evidenced temporal resource partitioning, and possibly the storage effect, a coexistence mechanism that requires environmental fluctuations (Chesson 2000).

The 'aggregation model of coexistence' states that when individuals of a species aggregate, they inhibit their own population growth more than they inhibit the population growth of other species, and that even when species use the same type of resource, their coexistence is facilitated where the distribution of individuals varies across patches (Hartley and Shorrocks 2002). This scenario is applicable to the aggregation patterns of dung beetles observed by Sullivan et al. (2017a,b). Furthermore, several earlier studies had reported that the interspecific aggregation of dung beetles is more common among biologically similar species than less similar species (Hanski 1987; Krell et al. 2003; Krell-Westerwalbesloh et al. 2004; Boonrotpong 2012). The recent work of Sullivan et al. (2017a,b) supports these historical findings and elaborates on them with multispecies correlation analysis.

In the studies of Sullivan et al. (2017a,b), the overall pattern of high correlations among tunnellers (Scarabaeinae) appears to have been primarily due to their aggregation in dung that was fresh, and had high moisture content, during their morning peak flight period

(Tables 2, 4). Mean abundance peaked between 12 h and 24 h after dung deposition and then rapidly declined (Tables 1, 3). In contrast, the mean abundance of dung dwelling species was much more uniform for dung deposition time and exposure period than for the tunnelling species, indicating a broader band of diel activity and tolerance of a wider range of dung moisture contents. Diel activity in dung beetles has been reported by many authors, including Hernandez (2002), Krell-Westerwalbesloh et al. (2004), Boonrotpong et al. (2012) and Sladecek et al. (2017). Krell-Westerwalbesloh et al. (2004) further reported that the diel separation of ball rolling species, and dung dwelling and tunnelling species, reduces the level of interguild competition.

In their studies, Sullivan et al. (2017a,b) did not examine whether diel activity, environmental filtering or competitive exclusion, or a combination thereof, drove phylogenetic clustering of the Scarabaeinae. However, the different patterns of diel activity and the age of dung preferred, which is directly related to the dung moisture content preferred, would have reduced the potential for the imposition of interference competition on the dung dwelling species by the tunneling species which are generally superior competitors. The less densely populated dung pads, or even segments of pads, in which inferior competitors experience less competitive pressure were termed 'probability refuges' by Shorrocks and Rosewell (1987) and 'temporal refuges' by Krell-Westerwalbesloh et al. (2004).

Dung moisture content has been identified as an ecologically important parameter in the short term structuring of dung beetle communities (Lumaret 1995; Sabu et al. 2006). The latter reported that the abundance of tunnellers increased with dung age and decreasing moisture content up to a threshold level, followed by a decrease, but dwellers did not show a significant relationship with dung moisture content. The results of Sabu et al. (2006) are supported by those of Sullivan et al. (2017a,b) in that the temporal decline in moisture content in pads excluded, or excluded to a relative extent, species of Aphodiinae and Scarabaeinae from pads at different times and thereby separately concentrated the pools of Aphodiinae and Scarabaeinaespecies and their abundances (Tables 1, 3). This scenario provides a mechanism through which environmental filtering may be contributing to underdispersion or clustering.

Closing remarks and conclusions

Animal dung, as small units of ephemeral, temporally and spatially dispersed resource, provides a convenient but complex environment for the study of community assembly and function at a fundamental level. In the studies of Sullivan et al. (2017a,b), diel activity, and then environmental filtering at the level of dung moisture content, appear to have been reflected in intraspecific and interspecific aggregation patterns that evidenced temporal resource partitioning between the Aphodiinae and Scarabaeinae. Diel activity and environmental filtering may therefore constitute mechanisms that are collectively driving community underdispersion or phylogenetic clustering. However, as reported by Lumaret et al. (1992) and Sullivan et al. (2017a,b), the number of co-occurring, abundant, closely related dung beetle species i.e., the extent of phylogenetic clustering, is restricted. That phenomenon was termed 'limiting similarity' by Hanski and Camberfort (1991).

Overall, the evidence presented in this perspective may indicate that niche differences were greater than fitness or competitive ability differences across the multiple combinations of dung dwelling and tunnelling dung beetle species reported by Sullivan et al. (2017a,b), which would provide an additional stabilizing mechanism to facilitate the coexistence of species. In conclusion, in contradiction of an element of both classical niche theory and the competition-relatedness theory, the very high correlations reported among abundant, congeneric, tunnelling dung beetle species within the subfamily Scarabaeinae in two experimental field studies lend support to the contemporary coexistence theory's postulate that increasing phylogenetic proximity, or relatedness, does not necessarily increase the probability of competitive exclusion.

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Table 1 Mean abundance (± SE) of two guilds of dung beetles in standardised dung pads in summer in the Kizilirmak Delta in Samsun Province, Turkey* (Sullivan et al. 2017a)

Dung deposition time	Tunnellers	Dwellers
06:00	185 ± 43a	9 ± 2a
10:00	71 ± 12b	11 ± 2a
14:00	66 ± 10b	13 ± 2a
18:00	27 ± 8c	11 ± 4a
22:00	77 ± 10b	7 ± 2a
02:00	76 ± 10b	6 ± 1a
Dung exposure period (h)	Tunnellers	Dwellers
12	92 ± 21ab	7 ± 1a
24	104 ± 19a	11 ± 2a
48	56 ± 9b	10 ± 1a

*In each sub-table, means followed by the same letter in the same column are not significantly different (Tukey's HSD, $P < 0.05$). Means are on the untransformed scale but significance is from the transformed analyses. For the tunnellers, deposition time and exposure period are independent

Table 2 Correlation coefficients for dwelling and tunnelling species in standardised dung pads in a summer assemblage of dung beetles in the Kizilirmak Delta in Samsun Province, Turkey* (Sullivan et al. 2017a)

	Ot	Of	Cs	Ep	Ef	tot.5t	On	Or	tot.7t	Ll	Ss	Oh	Ai	tot.4d
Ot	Ot													
Of	**_0.57_**	Of												
Cs	**_0.62_**	**_0.81_**	Cs											
Ep	**_0.45_**	**0.36**	_0.26_	Ep										
Ef	**_0.40_**	_0.28_	**_0.41_**	**_0.66_**	Ef									
tot.5t	NA	NA	NA	NA	NA	tot.5t								
On	-0.05	0.01	_0.24_	-0.05	**0.33**	0.06	On							
Or	0.05	_0.25_	**0.37**	0.15	**0.33**	_0.27_	**_0.72_**	Or						
tot.7t	NA	NA	NA	NA	NA	NA	NA	NA	tot.7t					
Ll	-0.16	-0.11	-0.20	-0.18	-0.20	-0.18	-0.02	-0.07	-0.18	Ll				
Ss	0.03	-0.01	-0.10	0.18	-0.05	0.00	-0.04	-0.01	0.00	0.13	Ss			
Oh	0.15	_0.27_	_0.24_	**0.33**	**_0.59_**	**0.32**	_0.24_	0.18	**0.33**	-0.21	-0.11	Oh		
Ai	-0.11	_-0.23_	-0.10	-0.19	-0.16	-0.21	-0.07	-0.19	-0.22	_0.27_	0.22	**-0.30**	Ai	
tot.4d	-0.07	-0.02	-0.12	0.04	0.03	-0.05	0.05	-0.02	-0.04	NA	NA	NA	NA	tot.4d

*Significance levels: $P < 0.05$ at $r = 0.23$; $P < 0.01$ at $r = 0.30$; $P < 0.001$ at $r = 0.38$
$P < 0.05$ (italicized), $P < 0.01$ (bold), $P < 0.001$ (bold and underlined)

Species with a mean number ≥ 0.2 / pad were included in the table: 1. Aphodiinae (dung dwellers): Ai= _Acanthobodilus immundus_, Ll= _Labarrus lividus_, Oh= _Otophorus haemorrhoidalis_, Ss = _Subrinus sturmi_; 2. Scarabaeinae (tunnellers): Cs= _Caccobius schreberi_, Ef= _Euoniticellus fulvus_, Ep= _Euoniticellus pallipes_, Of= _Onthophagus furcatus_, On= _Onthophagus nuchicornis_, Or= _Onthophagus ruficapillus_, Ot= _Onthophagus taurus_; tot.= total; t= tunneller; d= dweller, NA= not applicable

Table 3 Abundances (mean ± SE) of dwelling and tunnelling dung beetle species in standardised dung pads in the Kizilirmak Delta in Samsun Province, Turkey* (Sullivan et al. 2017 b)

	Tunnelling species			Dwelling species	
Exposure period (h)	Dung deposition time		Exposure period (h)	Dung deposition time	
	6:00	18:00		6:00	18:00
3	56 ± 6 ab*	26 ± 7 bc	3	1.5 ± 1 d	6.8 ± 3 c
6	86 ± 17 a	21 ± 4 bc	6	6.8 ± 2 c	3.8 ± 2 cd
12	87 ± 20 a	15 ± 6 bcd	12	8.8 ± 3 c	7.3 ± 1 c
24	52 ± 12 ab	73 ± 9 a	24	20 ± 6 b	20 ± 4 b
48	14 ± 3 bcd	10 ± 4 d	48	57 ± 6 a	49 ± 12 a
96	0	0.5 ± 0.5	96	13 ± 10 c	65 ± 22 a

*Within the tunnelling and dwelling species sub-tables, means followed by the same letter are not significantly different (Tukey's HSD, $P < 0.05$). Means are on the untransformed scale but significance is from the transformed analyses. The 96 hour exposure period data for tunnellers was excluded from the analysis and 192 h was excluded for both tunnellers and dung dwellers (only 1 specimen was collected at 192 h)

Table 4 Correlation coefficients of dwelling and tunnelling species of dung beetles in standardised dung pads in the Kizilirmak Delta in Samsun Province, Turkey* (Sullivan et al. 2017 b)

	Cs	Ot	Or	Of	Ep	On	Ef	Ce	Oo	Ov	tot.t	Ai	Bg	Ss	Pv	Em	Ll	Oh	tot.d
Cs	1.0																		
Ot	**<u>0.61</u>**	1.0																	
Or	**<u>0.54</u>**	**0.42**	1.0																
Of	**<u>0.70</u>**	**0.59**	**<u>0.77</u>**	1.0															
Ep	0.25	**<u>0.62</u>**	**0.44**	**0.38**	1.0														
On	0.25	**<u>0.56</u>**	0.02	0.14	***0.30***	1.0													
Ef	**<u>0.69</u>**	**0.59**	**<u>0.55</u>**	**<u>0.77</u>**	0.28	0.18	1.0												
Ce	***0.29***	0.19	**<u>0.74</u>**	**<u>0.61</u>**	0.20	0.0	**0.39**	1.0											
Oo	0.05	-0.08	**<u>0.48</u>**	0.27	0.17	0.18	0.09	**<u>0.65</u>**	1.0										
Ov	0.0	0.16	***0.30***	0.16	0.24	0.1	0.13	**<u>0.51</u>**	***0.33***	1.0									
tot.t	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1.0								
Ai	-0.11	***-0.31***	-0.15	***-0.31***	-0.22	-0.03	***-0.29***	-0.18	-0.01	-0.09	-0.25	1.0							
Bg	0.0	-0.02	0.16	-0.03	-0.18	-0.07	0.19	0.16	0.11	0.19	0.03	0.06	1.0						
Ss	**<u>-0.49</u>**	**-0.39**	-0.2	-0.27	-0.18	***-0.31***	-0.23	-0.10	-0.13	0.03	**-0.43**	-0.04	-0.03	1.0					
Pv	-0.17	0.23	-0.18	-0.20	***0.35***	**0.41**	-0.16	-0.12	-0.11	0.26	-0.03	0.23	-0.12	0.07	1.0				
Em	0.0	0.17	-0.05	-0.16	-0.02	-0.12	-0.11	-0.10	0.01	-0.18	-0.11	***0.35***	**0.43**	-0.13	-0.17	1.0			
Ll	-0.02	0.12	0.01	-0.11	***0.35***	**0.39**	-0.11	-0.14	0.17	-0.13	0.05	0.20	0.06	-0.11	**0.37**	0.03	1.0		
Oh	-0.03	0.13	0.28	0.13	***0.32***	-0.06	0.17	0.17	-0.08	0.02	0.14	0.21	-0.04	0.27	**0.37**	-0.15	0.17	1.0	
tot.d	**<u>-0.49</u>**	***-0.31***	-0.13	-0.26	-0.04	-0.23	-0.20	-0.08	-0.13	0.04	***-0.36***	NA	NA	NA	NA	NA	NA	NA	1.0

*Significance levels: P < 0.05 at r = 0.29 (bold and italicised); P < 0.01 at r = 0.37 (bold); P < 0.001 at r = 0.46 (bold and underlined)

Scarabaeinae (tunnellers): Cs= *Caccobius schreberi* (L.), Ef= *Euoniticellus fulvus* (Goeze), Ep= *Euoniticellus pallipes* (Fabricius), Of= *Onthophagus furcatus* (Fabricius), On= *Onthophagus nuchicornis* (L.), Oo= *Onthophagus opacicollis* Reitter, Or= *Onthophagus ruficapillus* Brullé, Ot= *Onthophagus taurus* (Schreber), Ov= *Onthophagus vacca* (L.); Aphodiinae (dung dwellers): Ai= *Acanthobodilus immundus* (Creutzer), Bi= *Bodiloides ictericus* ssp*. ghardimaouensis* Balthasar, Ce= *Colobopterus erraticus* (L.), Em= *Esymus merdarius* (Fabricius), Ll= *Labarrus lividus* (Olivier), Oh= *Otophorus haemorrhoidalis* (L.), Pv= *Planolinellus vittatus* (Say), Ss= *Subrinus sturmi* (Harold) (Aphodiinae); tot.= total; t= tunneller; d= dung dweller, NA= not applicable