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Temporal Resource Partitioning and Interspecific Correlations in a Warm, Temperate Climate Assemblage of Dung Beetles (Coleoptera: Scarabaeidae)

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Abstract

Guilds of dung dwelling and tunneling 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 resource partitioning in their coexistence. Standardized 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 tunneling and seven dung dwelling species were collected. The tunnelers contributed a high proportion of both total abundance and biomass. There was a significant effect of dung deposition time and exposure period on mean tunneler abundance. Mean tunneler 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 tunnelers by relatively uniform dispersal across the six dung deposition times. The distinctly different dung use patterns by dwellers and tunnelers demonstrated temporal resource partitioning. Interspecific correlation coefficients were also determined because interspecific relationships are at the core of resource partitioning. Total tunneler and dweller abundances were not correlated. Overall, there were strong positive correlations between tunneling species and low correlations between tunneling and dwelling species, and between dwelling species. The five most abundant tunnelers, from two tribes and three genera, were strongly positively correlated. There were substantial size differences among the four most abundant tunnelers that probably facilitate their coexistence.

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

Nichols et al. (2008) reported in a review that dung beetles provide ecological functions and ecosystem services in natural environments and agroecosystems in temperate, subtropical, and tropical environments by increasing 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; tunnelers 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 tunnelers (Doube 1990; Hanski and Cambefort 1991a; Krell et al. 2003). Dung dwelling species predominate in cool, temperate regions of the northern hemisphere (Hanski

and Cambefort 1991a; 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 tunnelers (Hanski and Cambefort 1991a), 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 aggregation 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 (1991) 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 tunneling, 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 tunneling species. Is temporal resource partitioning one of the mechanisms? That question was addressed by varying the time of deposition and the exposure period of standardized dung pads to determine whether they affect the mean abundance of the dwelling and tunneling species. In addition, correlation analysis was used to determine the strength of interspecific relationships and their overall pattern.

Materials and Methods

Study Site
The experiment was conducted in the Kizilirmak Delta in 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 at the time of the experiment. 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 was essentially sand containing a small amount of organic matter.

Experimental Conditions and Design
Sunrise and sunset were at 05:28 h and 19:53 h 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 h on 31 July 2015. 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 firmly packed underneath. Before deposition, the site for each pad was leveled by hand so that the pads were relatively flush with the soil surface. Standardized 1 kg pads (Rougon and Rougon 1991; Krell 2007) were formed in a plastic mold and deposited directly on the sand surface at 06:00, 10:00, 14:00, 18:00, and 22:00 h on 31 July 2015 and at 02:00 h on 01 August 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 × 3 × 4 pads = 72 pads in total). The four replicates were arranged in two rows containing two replicates, with 10 m between the rows. Within the rows, there was 6 m between the replicates, and within each replicate, there was 5 m between pads (Sullivan et al. 2016b). 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 h and 07:00 h on 2 August 2015.

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 tunnelers, 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, *Scarabaeus 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).

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 species level. Voucher specimens of all species collected are held at the Plant Protection Department, Faculty of Agriculture, Ondokuz Mayis University, Samsun, Turkey.

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 0.001 g. 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.

Statistical Analysis
To determine whether temporal resource partitioning had occurred, two-way analysis of variance (ANOVA) was used to examine the effects of dung deposition time and exposure period on mean dweller

Table 1. Abundance and biomass of dwelling and tunneling species in standardized dung pads in a summer assemblage of dung beetles in a warm, temperate coastal area of 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—tunnelers	**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; tunnelers: *Colobopterus erraticus* (L.), *Onthophagus opacicollis* Reitter, *Onthophagus vacca* (L.); dwellers: *Euheptaulacus carinatus* (Germar), *Nialus varians* (Duftschmid), *Pleurophorus* sp.

and tunneler abundance, after the data had been transformed to make the variance independent of the mean, and with the adjusted Least Significant Difference (LSD) test 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 tunnelers because on most occasions the activity of the ball roller *S. sacer* did not coincide with the collection times of the dung pads.

Results and Discussion

Species, Abundance and Biomass
In this study from the central Black Sea coast of Turkey, 6,669 adult dung dwelling and tunneling dung beetles, from 10 tunneling species in four genera and seven dung dwelling species in seven genera, were collected (Table 1). Two species, *E. carinatus* and *Pleurophorus* sp., which were not reported by Sullivan et al. (2016a), were collected in the present study. The tunnelers 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 and summer, small tunnelers regularly and strongly dominate abundance in dung beetle assemblages.

Dry Weight (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 tunnelers and dwellers collected was 67.4 g (Table 1), which was 0.6% of the total dry weight of the original dung.

Table 2. Mean abundance ($\pm$ SE) of two guilds of dung beetles in standardized dung pads in summer in a warm, temperate coastal area of northern Turkey

Dung deposition time	Tunnelers	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)	**Tunnelers**	**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 tunnelers, deposition time and exposure period are independent.

Effects of Dung Deposition Time and Exposure Period
In the present study, the deposition of dung pads at 4 h 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 tunneling guilds. Dung deposition time and exposure period were significant for mean tunneler 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 2). Mean tunneler 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 h than at 18.00 h ($P < 0.001$) across the three exposure periods, with the differences in mean dweller abundance non-significant in both cases.

Mean tunneler abundance for dung pads deposited at 06:00 h and 18:00 h was approximately 21 and 2.5 times higher,

Table 3. Correlation coefficients for dwelling and tunneling species in standardized dung pads in a summer assemblage of dung beetles in a warm, temperate coastal area of Turkey

	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 are included in the table: 1. Aphodiinae (dwellers): Ai = *Acanthobodilus immundus*, Ll = *Labarrus lividus*, Oh = *Otophorus haemorrhoidalis*, Ss = *Subrinus sturmi*; 2. Scarabaeinae (tunnelers): Cs = *Caccobius schreberi*, Ef = *Euoniticellus fulvus*, Ep = *Euoniticellus pallipes*, Of = *Onthophagus furcatus*, On = *Onthophagus nuchicornis*, Or = *Onthophagus ruficapillus*, Ot = *Onthophagus taurus*. tot. = total; t = tunneler; d = dweller, NA = not applicable.

respectively, than mean dweller abundance (Table 2). The dwellers dispersed much more uniformly across the six dung deposition times and three exposure periods than the tunnelers (Table 2), which meant they were able to occupy dung pads less densely populated with tunnelers, thereby reducing the potential for competition. These results reflect overall differences in the diel activity of tunnelers and dwellers and in the age of dung they are able to utilize. Furthermore, Lumaret and Kirk (1987) reported that (i) tunnelers and dwellers are generally spatially separated within the same dung pad in zones with different moisture content, which reduces inter-guild competition; (ii) tunneling 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.

Comparison of 2014 and 2015 Data

A study conducted by Sullivan et al. (2017) in mid-June, 2014 at the same site as the current study provides a broader perspective. The 2014 study had two of the same dung deposition times (06:00 and 18:00 h) 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 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, the five most abundant species in the dung pads deposited at 06.00 hours and exposed for 12, 24 or 48 h, in descending order of abundance, were *Subrinus sturmi* (Harold), *C. schreberi*, *O. taurus*, *Onthophagus ruficapillus* Brullé and *Otophorus haemorrhoidalis* (L.). In 2015, for the 12 equivalent pads, 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. Substantial changes in the suite of species and

their abundances in a short period were also reported by Lumaret and Stiernet (1991) and Jay-Robert et al. (2008).

Spatial Correlation of Dwelling and Tunneling Species

In the second component of the current study, the degree of aggregation of the commonest species was quantitatively investigated with correlation analysis. Specifically, interspecific (pairwise) correlation coefficients were determined for the 11 most abundant species, namely seven tunnelers 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 tunneler and dweller abundances were not significantly correlated. However, the five most abundant tunnelers 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 3). *O. taurus*, which was the largest and most abundant tunneler, contributed 34% of all individuals and 63% of total biomass. It was also highly and positively correlated with the next four most abundant tunnelers ($P < 0.001$). Overall, the highest correlation was between *O. furcatus* and *C. schreberi* ($P < 0.001$) (Table 3). Hanski (1991) reported that strong positive correlations indicate 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 that competition and facilitates coexistence.

Size of Tunneling 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 tunneling species (Table 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 tunneler was in class 4, but it represented only 3% of total abundance and 5% of total dry biomass. The least abundant tunnelers, *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 tunnelers were lower and variable, and particularly low with *O. taurus* (Table 3).

The question arises as to the reason for the generally high, positive correlations among tunneling 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.

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 tunnelers. *O. haemorrhoidalis* was atypical in that it was significantly and positively correlated with five of the seven tunnelers, and negatively and significantly correlated with *A. immundus* (r = −0.30; $P < 0.05$) (Table 3). In contrast, *S. sturmi* was not significantly correlated with any species, with most individuals collected when the activity of tunnelers 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 standardized dung pads in Ireland. In contrast, Holter (1982) reported positive associations for *Aphodius* species in standardized 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).

Coexistence of Tunneling and Dwelling Species

Coexistence is facilitated by the increased aggregation of competitively superior 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) referred to these lower density sites as "probability refuges." In the present study, the high variability of mean tunneler abundance (Table 2) would have made lower density sites (probability refuges) available to the dwelling species, which tend to be inferior competitors, thereby increasing their relative competitiveness and breeding opportunities. Furthermore, Hanski and Cambefort (1991b) reported that the relatively small size and high fecundity of inferior competitors help them avoid exclusion from the local species pool, even at high levels of competition.

Concluding Remarks

The present study demonstrated markedly different dung use patterns by dung dwelling and tunneling species across six dung deposition times and three exposure periods that evidenced temporal resource partitioning. Correlation analysis revealed the pattern of interspecific relationships underpinning that partitioning, with the tunneling species showing a strong tendency to positively associate, and the dwelling species tending to avoid both the tunneling species and other dwelling species, except in one case. The current study was designed to examine interspecific and interguild relationships temporally, rather than determine whether intra- and interspecific aggregation patterns were actually reducing competition and facilitating coexistence, as did the studies by 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 coexistence and supporting the maintenance of dung beetle diversity in the Kizilirmak Delta of Turkey and in warm, temperate climate dung beetle assemblages generally.

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