

Patterns of Niche Partitioning and Alternative Reproductive Strategies in an East African Dung Beetle Assemblage

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Abstract Sympatric species of coprophagous dung beetles rely on essentially the same resource for provisioning broods, which raises the question of how local species diversity is maintained. Interspecific competition may be mitigated to some extent by large-scale spatial (e.g., habitat type) and temporal (e.g., seasonal) variation in activity. Niche partitioning also occurs at the scale of individual dung pads. We examined the extent to which inter- and intraspecific variation in adult morphology and behavior contribute to spatial and temporal partitioning above and below the dung pad in the dung beetle community of Kibale Forest, Uganda. Excavations in the vicinity of dung pads revealed significant heterogeneity among species and guilds in the lateral distance between tunnels and dung, and in tunnel depth. Patterns of succession and diel activity demonstrated strong temporal dissociations among guilds. In one species, *Onthophagus multicornis*, we found a bimodal distribution of male horn sizes and a tunneling pattern consistent with alternative reproductive tactics.

Keywords Dung beetles · Kibale National Park · niche partitioning · *Onthophagus multicornis* · reproductive strategy

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Mammalian dung is a high quality, but scattered and ephemeral, resource that supports many of the over 8,000 species of coprophagous dung beetles (Coleoptera: Scarabaeoidea; *ScarabNet Global Taxon Database version 1.5*). Within local species assemblages, dung beetles exhibit niche partitioning along several ecological axes (Hanski and Cambefort 1991a), including dung colonization times (Hanski 1980a), seasonality (Hanski 1980b; Jay-Robert et al. 2008), diel activity (Krell-Westerwalbesloh et al. 2004), trophic preferences (Martin-Piera and Lobo 1996), as well as in foraging and nesting strategies (Cambefort and Hanski 1991). Species-specific dung preferences have been documented based on dung odour (Dormont et al. 2010), dung type (within and among trophic levels; Lumaret and Iborra 1996; Finn and Giller 2002), age (Doube 1987), and water content (Sowig and Wassmer 1994). Niche partitioning also occurs at the scale of individual dung pads (Halffter and Matthews 1966; Holter 1982; Edwards and Aschenborn 1987).

Dung beetles can be classified into guilds or functional groups (FG) based on modes of foraging and dung burial (Doube 1990). Telecoprids (referred to here as ‘rollers’) roll away small portions of dung before burying and laying eggs in them, whereas endocoprids lay eggs directly within the dung, and paracoprids (referred to here as ‘tunnelers’) construct nests under the dung pad prior to laying eggs. Kleptocoprids lay eggs in dung buried by other dung beetles. Functional categorization can be further broken down by body size, which is a strong predictor of competitiveness (Moczek and Emlen 2000; Safryn and Scott 2000). This system provides a framework for analyzing the structure of many dung beetle communities (for example, Giller and Doube 1994; Krell and Krell-Westerwalbesloh 2003).

The local partitioning of resources below individual dung pads is less well known (but see Holter 1982; Cambefort and Hanski 1991), perhaps due to the inherent difficulties in observing underground activity. Tunnelers construct nests at different positions below and away from the dung pad, and there are clear differences in nest architecture between species (Halffter and Edmonds 1982). Underground stratification of nest sites may serve to optimize each inhabitant’s reproductive efforts and may also help to mediate coexistence of species with similar life histories.

Underground distribution may also reflect differences in reproductive strategies within species. Intense intra-sexual competition is thought to have resulted in the evolution of alternative mating tactics in male dung beetles (Emlen et al. 2005), where small males (minors) may gain little from direct competition with large males (majors) and instead adopt a ‘sneaker’ strategy of opportunistic copulation (Eberhard 1982).

The aims of this study were to: (1) characterize the activity patterns and nesting behavior of an East African dung beetle assemblage; (2) document patterns of spatial and temporal partitioning above and below the dung pad; and (3) examine the relationship of these phenotypes with corresponding inter- and intraspecific variation in morphology.

Methods

Study Site This study was conducted in and around the Makerere University Biological Field Station (MUBFS) located within Kibale National Park, western Uganda (766 km²; 0°13′ to 0°41′ N and 0°19′ to 30°32′ E). The Kibale forest is a medium-altitude moist forest that is a mosaic of tall evergreens, swamp, thickets and

grasslands. Kibale averages 1,670 mm of rainfall per year with two rainy seasons, in March to May and September to November (Shepherd and Chapman 1998). This study was conducted from the 6th to the 23rd of February of 2009, which coincides with the end of the dry season.

Despite its fragmented landscape, the mammalian fauna of Kibale is still one of the most diverse and relatively intact communities in the tropics. 23 mammalian families are represented in Kibale. Its 11 species of primates make up one of the highest populations and biomass densities of primates anywhere in the world (Oates et al. 1990). The accompanying range and abundance of mammalian dung is likely to serve to enhance the diversity of the dependent dung beetle fauna.

Classification of Beetles and Species Identification When characterizing dung beetle communities, it is useful to group species into guilds based on modes of foraging and dung burial. We used a modified version of Doube's (1990) system of classifying species into functional groups (FG) according to mode of dung acquisition (roller or tunneler) and size (large or small) (Table 1). According to Doube's classification, FG III include smaller tunnelers, while FG IV include larger tunnelers. We were not able to classify the tunnelers *Heliocopris haroldi* and *Onitis viridulus* in this way due to insufficient behavioral observations.

Digital photographs were taken of specimens captured in the vicinity of MUBFS using a 100 mm macro lens and sent to Philippe Moretto for species

Table 1 Summary of identified species sorted by guild and functional group

Guild	FG	Species	Counts	Size (mm)	Dung type
Rollers	I	<i>Garreta crenulatus</i> Kolbe	60	11.41 (58)	E & P
	I	<i>Anachalcos cupreus</i> Fabricius	5	ca. 13	E & P
	II	<i>Sisyphus</i> sp.	28	ca. 5	P
Tunnelers	III	<i>Onthophagus (Proagoderus) multicornis</i> d'Orbigny	213	7.32 (154)	E & P
	III	<i>Onthophagus mixtidorsis</i> d'Orbigny	88	ca. 7	E & P
	III	<i>Onthophagus fuscidorsis</i> d'Orbigny	25	ca. 5	E & P
	IV	<i>Catharsius ninus</i> Gillet	69	8.86 (55)	P
	IV	<i>Onthophagus (Diastellopalpus) semirubidus</i> d'Orbigny	61	11.50 (40)	E & P
	IV	<i>Onthophagus (Diastellopalpus) gilleti</i> d'Orbigny^a	11	11.57 (3)	E & P
	-	<i>Heliocopris haroldi</i> Kolbe	4	ca. 25	E
	-	<i>Onitis viridulus</i> Boheman	3	ca. 11	E

Species names follow ScarabNet Global Taxon Database version 1.5 (<http://216.73.243.70/scarabnet/results.htm>). Species in bold are discussed in the text. **Counts** are the total observed and recorded individuals for all parts of this study. **Size**: mean elytra width with number of individuals measured in parentheses. **Dung type**: E=sampled in elephant dung, P=sampled in primate dung. **FG**: I=large telecoprids, II=Small telecoprids, III=small, early-appearing paracoprids, IV=larger, late-appearing paracoprids

^a first record in Uganda

identification. Identification of some beetles beyond the generic level was not possible, including a few *Sisyphus* species (Table 1). Elytra width and horn length were measured on dung beetles collected from dung pads from both human and naturally occurring primate and elephant dung. One person (AC) performed all measurements with dial calipers to varying levels of precision, depending on species, morph and body part (Table 1).

In Situ Observations Diurnal species-specific arrival times and above-ground behaviors were recorded at 12 sites. All sites were located in areas of recent primate sightings (< 2 days) near MUBFS. Roughly 60 ml of fresh human feces (< 3 days old) was placed in the center of a circular clearing (approximate radius 30 cm) of shaded forest floor at 09:30. Behavioral observations were either carried out immediately after placement of feces at 6 sites or starting 1-hour post-placement at the other 6 sites. Each observation session lasted 2 continuous hours (i.e., 09:30–11:30 or 10:30–12:30).

The 12 sites used for above-ground observations and 3 additional sites were randomly assigned to be excavated at 5, 24, or 48 h after placement of dung. Five excavations were completed at each time (15 excavations total). Excavations involved first recording the presence of beetles above ground, then systematically unearthing the surrounding soil, beginning 30 cm away from the approximate center of the dung pad, at a depth of no less than 10 cm. Excavations proceeded inwards until the entire pad had been removed and sifted through by hand. Data on morpho-species and corresponding depth and distance from center of dung pad were recorded for each individual beetle.

Experimental Observations To investigate diel separation in Kibale's dung beetle community, above-ground activity was observed around the clock in an observation enclosure for seven commonly occurring species: *Onthophagus multicornis* ($N=106$), *O. mixtidorsis d'Orbigny* ($N=32$), *O. semirubidus* ($N=15$), *O. gilleti d'Orbigny* ($N=4$), *Garreta crenulatus* ($N=35$), *Catharsius ninus* ($N=21$), *Anachalcos cupreus* ($N=5$). All beetles were collected from naturally occurring primate and elephant dung pads and were allowed to intermingle in a plastic container (40×30×20 cm) filled with approximately 4 cm of soil and covered with breathable plastic netting. Beetles were thus allowed to move freely above and below ground but with restricted flight. Approximately 90 ml of non-human primate dung was provided daily at around 9 am and the number of active individuals and species above ground was counted via hourly scan sampling. An individual was regarded as active if it was above ground and moving. Three sets of 24-hour activity observations were conducted, with hourly sampling. Samples were not necessarily collected in consecutive hours, but rather, completed over the course of 7 days.

Statistical Methods Hierarchical ANOVA, with species nested within guild, was used to test for heterogeneity in arrival times among guilds and among species within guilds; arrival time was square-root transformed for this analysis to normalize the residuals. Likewise, hierarchical ANOVA, with species nested within tunnel functional group, was used to test for heterogeneity among groups in tunnel depth and

distance of tunnels from the dung pad. Chi-square tests of independence were used to test for differences among guilds in the temporal and spatial distributions of beetles at dung pads.

We used a segmented regression model (Eberhard and Gutiérrez 1991) to describe male horn allometry in *Onthophagus multicornis* using R 2.8.1 (The R Foundation for Statistical Computing <http://www.R-project.org>), in which X and Y are measurements of elytra width and horn length, respectively. We searched for a switch point by adjusting the Ψ parameter of the model (R function “segmented()”) incrementally, and selecting the best model based on AIC. We then compared the best fitting segmented regression model with a linear and logarithmic model, again using AIC as the criterion for selecting the best model (Okada et al. 2008). We used nonparametric Kruskal-Wallis, Wilcoxon, and Levene’s tests when the data appeared to violate parametric assumptions of normality or homoscedasticity.

Results

Local Fauna A total of 567 individuals of 11 species, belonging to 7 genera, were collected and identified (Table 1). Paracoprids (tunnelers) represented the majority of the Kibale dung beetle community (6 of 9 species that could be classified). No observed species exhibited the endocoprid strategy of nesting in the dung itself. The smaller species within *Onthophagus* and *Sisyphus* were the most abundant members of the tunneling and ball-rolling guilds, respectively.

Succession Roller species arrived sooner after dung placement than tunneler species (Table 2; guild $F_{1,117}=6.64$, $P=0.01$; species nested within guild $F_{4,117}=1.15$, $P=0.34$; $R^2=0.10$; excluding the two species with no replication). Rollers and tunnelers also differed in their temporal distribution below the dung pad over the 5–48 h excavation period (Chi-squared test, $\chi^2=7.48$, $df=2$, $P=0.024$). Only 3 of 55 arriving rollers were still present at the dung pad by 5 h after dung placement and none were present at the 24 and 48-hour marks (Table 3).

Table 2 Arrival times

	Guild	FG	Counts	Range	Mean	S.E.
<i>Anachalcos cupreus</i>	R	I	1	n/a	15	n/a
<i>Garreta crenulatus</i>	R	I	11	5 – 120	43	12
<i>Sisyphus sp.</i>	R	II	26	10 – 160	58	7
<i>Onthophagus fuscidorsis</i>	T	III	16	22 – 165	67	10
<i>Onthophagus multicornis</i>	T	III	17	11 – 163	70	10
<i>Onthophagus mixtidorsis</i>	T	III	47	5 – 166	86	7
<i>Onthophagus gilleti</i>	T	IV	1	n/a	23	n/a
<i>Onthophagus semirubidus</i>	T	IV	6	10 – 155	75	22

Arrival times (in minutes) of beetles arriving on the surface of the dung pad within the first 3 h of dung placement. The two species with no replication were omitted from the statistical analysis. T=tunneler, R=roller

Table 3 Summary of excavations by functional group

		5 h	24 h	48 h
Number of individuals, sorted by FG, present on or under dung pad at 5, 24 and 48 h post-placement of dung	<i>Rollers (FG I & II)</i>	3	0	0
	<i>Large tunnelers (FG IV)</i>	0	54	32
	<i>Small tunnelers (FG III)</i>	52	46	3

The temporal distributions of beetles of FG III and FG IV below the dung pad differed significantly ($\chi^2=75.95$, $df=2$, $P<0.001$; Fig. 1). Small tunnelers (FG III) were abundant below the dung pad at the 5 h and 24 h marks but virtually disappeared by 48 h post-placement (Table 3). In contrast, large tunnelers (FG IV) were not recorded until 24 h post-placement and were present at least until 48 h post-placement (Table 3).

In the observation enclosure, rollers (FG I) were most active above ground during daylight hours (Fig. 2), while the tunneler *Catharsius ninus* (FG IV) showed the mirror opposite pattern. Tunnelers (FG III and FG IV) showed sporadic activity, mostly under daylight. Most species of FG IV, except *Catharsius ninus*, tended to be crepuscular.

Spatial Separation Below Dung Pad Excavations in the vicinity of dung pads revealed significant heterogeneity among species in the lateral distance between tunnels and dung pads (one-way ANOVA, $F_{5,88}=5.12$, $P<0.001$, $adj R^2=0.18$) and in tunnel depth ($F_{5,88}=11.26$, $P<0.001$, $adj R^2=0.35$). The larger, later-appearing species in FG IV dug tunnels significantly farther from the dung pad and at greater depths than species in FG III (ANOVA with species nested within FG tunnel distance: FG term $F_{1,88}=16.43$, $P<0.001$, $adj R^2=0.18$; tunnel depth FG term $F_{1,88}=27.56$, $P<0.001$, $adj R^2=0.42$; Fig. 3a,b). Across species, mean body size (as measured by elytra width) correlated positively with mean distance between tunnel and dung pad

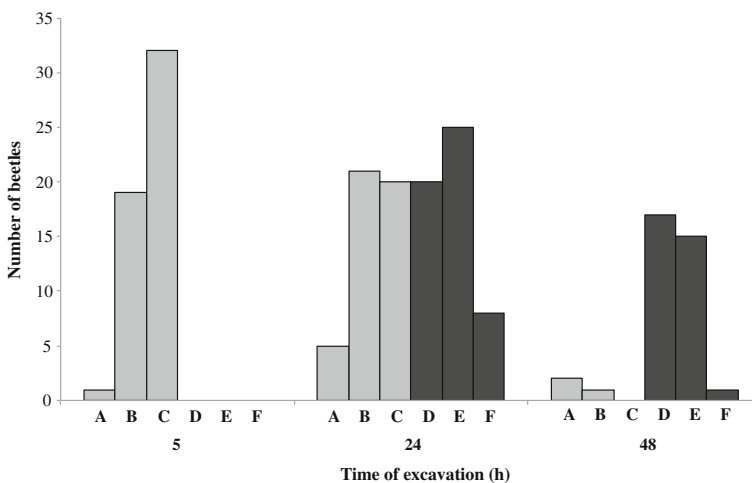


Fig. 1 Temporal distribution of tunnelers categorized by functional group. Light shading: FG III. Dark shading: FG IV. Species codes: a, *Onthophagus fuscicornis*; b, *O. mixtidorsis*; c, *O. multicornis*; d, *Catharsius ninus*; e, *O. semirubidus*; f, *O. gilleti*

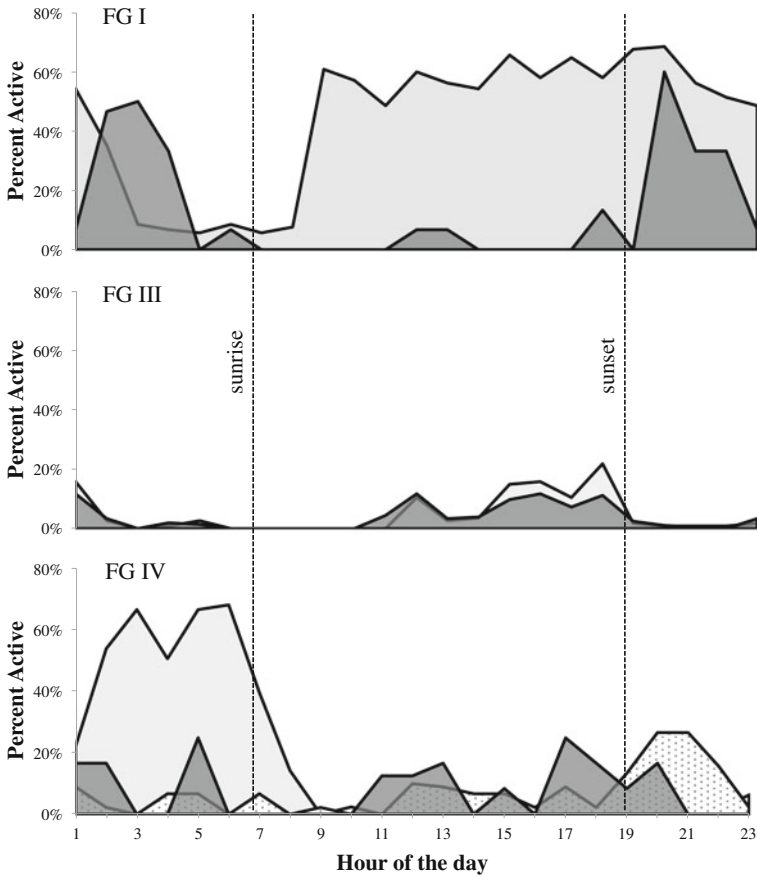


Fig. 2 Surface activity pattern of seven commonly occurring species, grouped by functional group. **Percent Active:** percent of individuals active out of total number within species. **FG I:** *Garreta crenulatus* ($N=35$, light grey), *Anachalcos cupreus* ($N=5$, dark grey); **FG III:** *Onthophagus multicornis* ($N=38$, light grey), *O. mixtidorsis* ($N=68$, dark grey); **FG IV:** *Catharsius ninus* ($N=21$, light grey), *Onthophagus gilleti* ($N=4$, dark grey), *O. semirubidus* ($N=15$, dotted). Sunrise was at 06:50 and sunset was at 18:56, approximately

($r=0.89$, $P=0.018$, $N=6$) but not with mean tunnel depth ($r=0.52$, $P=0.29$, $N=6$). Neither tunnel distance nor tunnel depth correlated significantly with body size within species (for all 12 correlations, $P>0.05$).

Alternative Reproductive Behavior of a Tunneler Onthophagus multicornis was the most rapid and common diurnal dung burrier. Horn lengths in male *O. multicornis* showed a continuous, bimodal distribution ranging from less than a 1 mm up to 8.56 mm in length (Fig. 4). Male elytra width also showed a faint bimodality (Fig. 5). Larger males possessed horns protruding from the head, whereas smaller males had shorter or vestiges of horns. The relationship between horn length and body size (Fig. 6) was best fit by a segmented linear regression with a switch point at an elytra width of 7.74 mm (AIC scores: segmented 172.93; logarithmic 178.56; linear 181.04). We used this switchpoint to separate males into either “majors” (with elytra width greater than 7.74 mm) and “minors” (with elytra width less than 7.74 mm), and

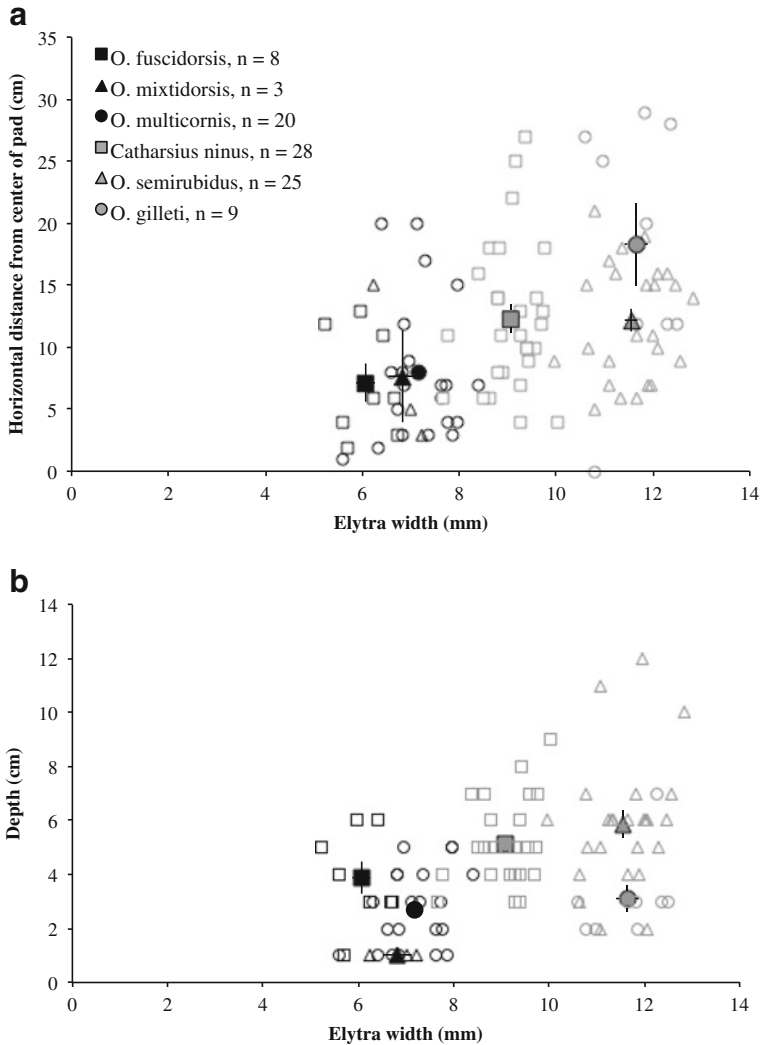


Fig. 3 Spatial distribution of individuals (open points, $N=93$) and species (filled points, mean, SE) within the tunneling community in terms of horizontal distance away from center of dung pad (a) and depth (b). Black filled/outlined points: FG III; Grey filled/outlined points: FG IV

determined whether the difference in male morph coincided with a change in behavior as approximated by our data on tunneling patterns.

We excavated 52 individuals of *O. multicornis* from the dung pads, all of which were found during the 5 and 24-hour mark (none were found at the 48-hour mark). There was a significant temporal difference between female, majors and minors (Kruskal-Wallis rank sum: $H=7.188$ $df=2$, $P=0.027$). Specifically, majors arrived later than both minors (Wilcoxon test: $N=33$, $W=153$, $P=0.026$) and females (Wilcoxon test: $N=28$, $W=41.5$, $P=0.013$). The number of females and minors decreased, and the number of majors increased from the 5-hour mark (female: 14, minor: 16, major: 2) to the 24-hour mark (female: 5, minor 8, major: 7), and this shift in composition was statistically significant (Chi-squared test, $\chi^2=7.329$, $df=2$, $P=0.026$).

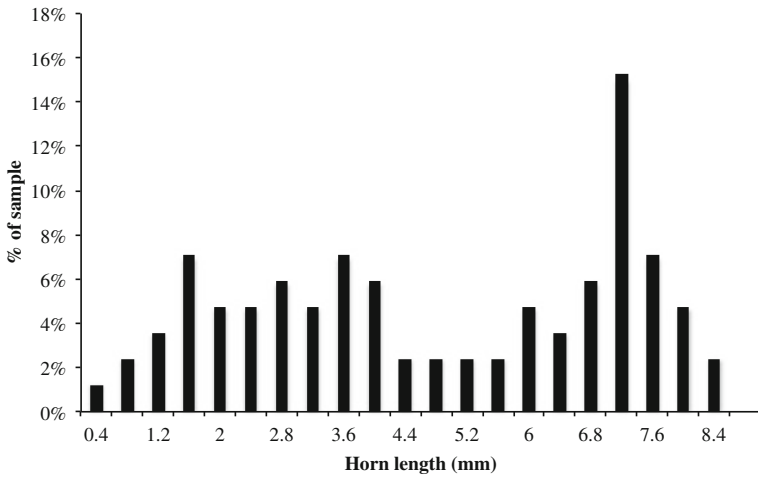


Fig. 4 Distribution of horn length of male *O. multicornis* is continuous and bimodal. Horn lengths ranged from 0.64 mm to 8.53 mm, with a mean of 4.97 mm and median of 4.83 mm ($N=85$). For analysis, the median horn length was used as an estimation of the cut-off point between male morphs: minors ($N=43$, < 4.83 mm); majors ($N=42$, > 4.83 mm)

Furthermore, horn length and elytra width increased with time from the 5-hour mark to the 24-hour mark (Wilcoxon test: $N=33$, $W=79$, $P=0.043$; $N=33$, $W=73$, $P=0.026$, respectively).

We observed no significant overall spatial separation between the three groups (females, minors, and majors), in horizontal distance from the dung pad (Kruskal-Wallis test: $H=3.913$, $df=2$, $P=0.141$), nor in vertical distance below the dung pad ($H=0.108$, $df=2$, $P=0.948$). No significant difference in horizontal distance from the dung pad (distance) and vertical distance below the dung pad (depth)

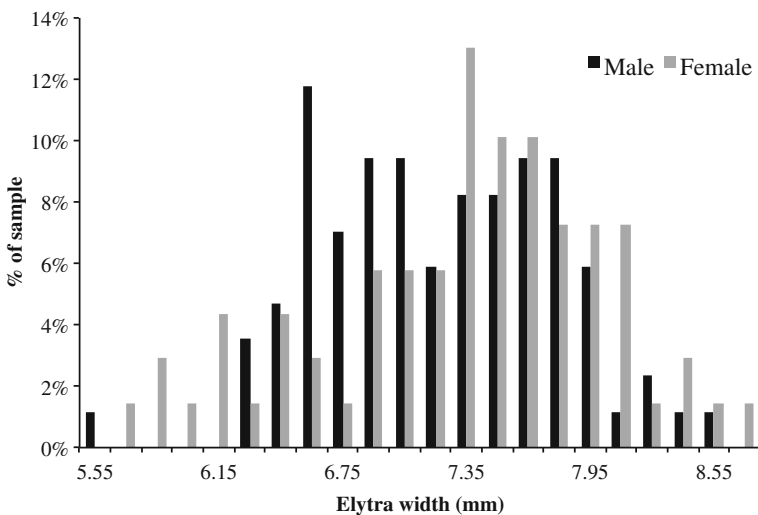


Fig. 5 Male *O. multicornis* elytra width show a slight bimodal distribution ($N=85$), in contrast to those of female *O. multicornis* ($N=69$)

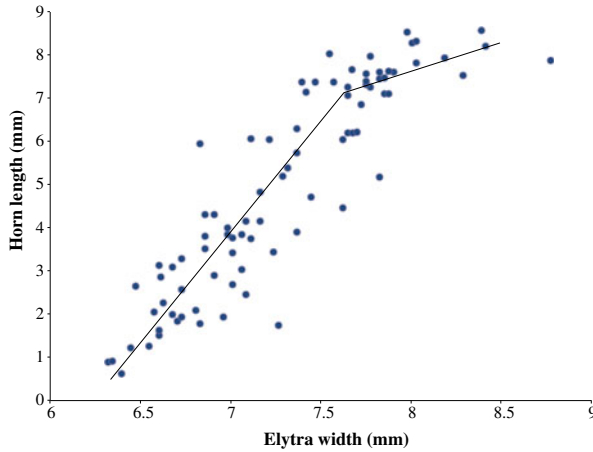


Fig. 6 Male horn allometry of 85 male *O. multicornis* analyzed via a segmented regression model (as in Eberhard and Gutiérrez 1991). A switchpoint occurs at elytra width of 7.75 mm

was observed between females and males (Wilcoxon test: $N=52$; distance: $W=216.5$, $P=0.065$; depth: $W=297$, $P=0.756$) and between majors and minors (Wilcoxon test: $N=33$; distance: $W=92$, $P=0.529$; depth: $W=109$, $P=0.9835$). No significant overall variance in horizontal or vertical tunnel location was found (Levene test: $F=3.537$, $df=2$, $P=0.057$; $F=1.302$, $df=2$, $P=0.281$, respectively). Nevertheless, males occupied a wider variation of horizontal tunnel positions than females did (Levene test: $F=7.053$, $df=1$, $P=0.011$; Fig. 7).

Discussion

Local Fauna All data were collected during the end of the long dry season, which most likely explains the lower species count compared to a previous study that recorded 14 species in the same selectively felled forest (Nummelin and Hanski

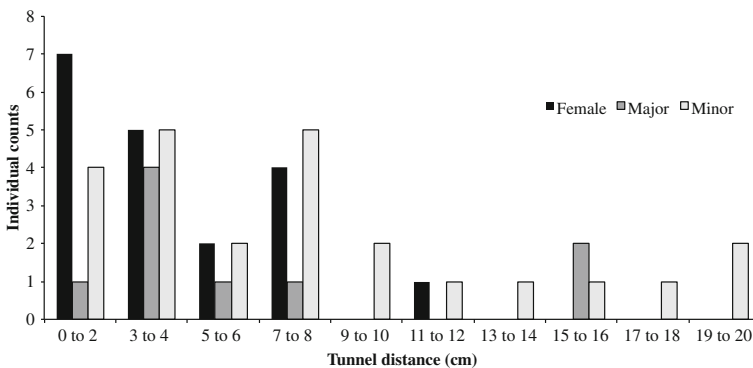


Fig. 7 Tunnel distances away from center of dung pad of different *O. multicornis* morphs and sex. Female $N=19$, majors $N=16$, minors $N=17$. Distance away from dung: females, $\mu=4.3$ cm SE=0.6 ; majors, $\mu=6.3$ cm S.E.=1.3, minors, $\mu=8.4$ cm S.E.=1.5

1989). As observed in previous studies in the forests of Uganda (Nyeko 2009), small-bodied, earlier appearing species (FG III) were the most abundant, constituting 326 of 567 documented individuals.

Spatial Separation Most studies of spatial partitioning in dung beetles have been concerned with large-scale (i.e., across regional habitats, across dung-pads) distributions of coexisting species (Hanski 1980a; Cambefort and Hanski 1991). Intraspecific aggregation across dung pads is well documented and has been argued to foster coexistence of competing species (Holter 1982; Giller and Doube 1994; Hutton and Giller 2004). We studied spatial partitioning of beetles within dung-pads and found that intraspecific aggregation occurs at this scale as well. Interspecific variation in body size appears to play a key role in determining the spatial distribution of tunnelers below the dung pad. Specifically, late-appearing species nested farther and deeper than smaller, early-appearing species.

Species-specific patterns in tunnel and nest structure (Halffter and Matthews 1966; Edwards and Aschenborn 1987), and in nesting location relative to the dung pad (Holter 1982), may reflect past interspecific competition, or interspecific competition during seasons of higher beetle abundance and diversity, or reproductive interference (Holter 1982; Gröning and Hochkirch 2008). Larval development time is long and resource intensive in rollers and tunnelers (Holter 1975) and is hampered by competitive interactions due to high beetle density (Holter 1979). Spatial separation of oviposition sites may reduce both direct (interference) and indirect (exploitative) competition and may also help protect broods from predators, parasites, and pathogenic fungi (Hanski and Cambefort 1991b). These explanations for spatial differentiation do not necessarily predict a size-dependent pattern of nesting locations between species and guilds, however.

We found that larger species of tunnelers nested farther from the dung pad than smaller species. We can think of three non-mutually exclusive explanations for this trend. First, physiological constraints imposed by body size, combined with a trade-off between the costs of digging tunnels and transporting dung versus the benefits of ovipositing farther from the dung pad, may result in a greater optimal distance for larger species. Large species are able to maintain higher internal body temperatures and consequently can move faster than small species (Chown and Klok 2011). For small species, the benefits of ovipositing farther from the dung pad (e.g., lower larval competition) may not be sufficient to offset the additional energetic costs and risks associated with constructing more extensive tunnels and transporting dung above ground (e.g., predation, parasitism). Second, larval competition increases with larval density, and may affect the organization of oviposition sites. The rate of oviposition decreases with increased adult density (Holter 1979) and larval mortality rate increases with number of eggs in a dung pad (Hirschberger 1998). Larvae of large species may be more vulnerable to competition because they are slower to develop, resulting in a greater optimal distance from the dung pad for larger species. Finally, the correlation between size and distance from the dung pad may arise simply because late-arriving beetles need to nest farther away to avoid competition with early-arriving beetles. Further research will be required to determine which factor, or combination of factors, best accounts for the observed spatial patterns.

Temporal Separation Temporal resource partitioning was observed between diurnal rollers (telecoprids) and tunnelers (paracoprids). Rollers were the first to arrive (< 3 h) and tunnelers dominated the dung pad community soon after (> 5 h). Another distinction arose later on; smaller tunnelers arrived and left earlier than their larger counterparts (Table 3). This pattern is consistent with that found in a local assemblage in southern Africa, where Doube (1990) observed that smaller tunnelers (FG III) interact approximately 6–24 h with the dung pad prior to departing, while larger tunnelers (FG IV) can remain up to 6 weeks.

At the proximate level, these temporal displacements may reflect guild-specific preference in dung freshness (as in Yasuda 1987; Doube et al. 1988). The ultimate reason may be that rollers need to arrive early to compete effectively with tunnelers. The rate of dung accumulation for rollers is severely limited by the time it takes to cut, roll and store a ball safely away from the source. This highly energetic form of foraging may require high body temperatures. The rate of ball rolling is dependent on body temperature (Bartholomew and Heinrich 1978), which may be prohibitively low at night. Indeed rollers were most active during daylight hours (Fig. 2). Nocturnal tunnelers, such as *Catharsius ninus* (Fig. 2), may avoid competition with the competitively superior diurnal ball rollers by exploiting the temporal refuges left by such constraints (Walter 1985; Krell-Westerwalbesloh et al. 2004).

Tunnelers were slow to arrive, but what temporal advantage they lose to rollers, they may regain through a larger inherent capacity to horde dung (Halffter and Edmonds 1982). Likewise, larger tunnelers appeared under the dung pad later than smaller tunnelers, but are capable of gathering more dung (up to 1000x the mass of the beetle; Doube 1990). Perhaps small species exemplify a scramble competition strategy while large species exemplify a contest competition strategy. For larger species, being competitive at the dung pad necessitates large body size (Moczek and Emlen 2000; Safryn and Scott 2000), which in turn demands greater accumulation of dung per brood. Small species demand less dung per brood and can effectively outcompete larger species by sheer numbers. When this is not the case, as in this study, smaller species require effective strategies to avoid direct competition, such as arriving before larger species monopolize the dung pad.

Alternative Mating Strategy in *Onthophagus multicornis* Dimorphisms in dung beetle horn lengths, particularly in the genus *Onthophagus*, are frequently associated with alternative reproductive behaviors. In some well-studied species (e.g., *O. acuminatus*, *O. taurus*, *O. binodis*), larger horned males, termed majors, defend tunnels against other males and in some cases help residing females with brood mass construction. In contrast, smaller horned males, termed minors, avoid direct confrontation with majors and attempt sneak copulations (Cook 1990; Emlen 1997; Hunt and Simmons 2000). Our morphological measurements and field observations are consistent with a similar pattern of alternative reproductive tactics in *O. multicornis*. Minors arrived earlier than majors, which may enable them to copulate with undefended females. Minors also occupied a wider range of lateral tunnel positions than both females and majors (Fig. 7). While these observations support the hypothesis of alternative male reproductive tactics in male *O. multicornis*, additional research is clearly needed to fully characterize the alternative tactics of this species.

Horn dimorphisms in *Onthophagus* are commonly underlain by a sigmoidal relationship between horn size and body size (Emlen 1994, 2008; Hunt and Simmons 1997; Moczek and Emlen 1999; Rowland and Emlen 2009). Abrupt changes in horn length have been shown to correspond with the switch from sneaking to fighting tactics (Hunt and Simmons 2000), and may be indicative of a developmental reprogramming event (Emlen and Nijhout 2000, 2001). We did not find a sigmoidal relationship in *O. multicornis*. Instead, horn length increased linearly with body size up to a point, above which the slope of the allometry decreased noticeably. This scaling relationship was best fit by a segmented regression model with one switchpoint (Fig. 6). Whether this relatively subtle shift in horn development corresponds with a switch in behavioral tactics remains to be determined.

Synopsis We found evidence for fine-scale niche partitioning within and between guilds in the dung beetle assemblage of Kibale forest, Uganda. We also uncovered what appears to be an alternative male reproductive strategy in one tunneling species (*O. multicornis*). We hope our findings stimulate further research on the surprisingly understudied dung beetles of East Africa.

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