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ORIGINAL ARTICLE

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

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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* Linnaeus was recorded in the Kizilirmak Delta on the Black Sea coast of Turkey by using artificial 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 balls (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.

INTRODUCTION

Ball production and rolling in dung beetles probably evolved to expedite escape from intraspecific and interspecific competition at the dung pad (Halffter & Matthews, 1966; Scholtz, 2009), and is a characteristic behaviour of the Scarabaeini of Scarabaeidae (Cambefort, 1991). Hanski & 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 & Matthews, 1966) and food balls tend to be smaller than brood balls (Hanski & Cambefort, 1991a). In a specific case, Edwards & 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 & 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 & Cambefort, 1991a] to 30 g in *Scarabaeus sacer* Linnaeus (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 & 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 & 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 artificial pads because their source, size and shape can be predetermined. In a study that did not include rollers, Barth et al. (1994) reported few differences in the communities of insects colonizing natural and artificial pads. Krell et al. (2003) used artificial 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 (Löbl & 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 & 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 the effects of dung pad size on the number and size of balls produced by *S. sacer*, and their time of production.

MATERIALS AND METHODS

Study site

The experiment was conducted along the exposed ridge line of a coastal sand dune (41°39′26″N, 36°04′03″E) adjacent to the Kizilirmak Delta on the central Black Sea coast of Turkey in early June, 2014. The sparse vegetation on the dune was dominated by *Euphorbia terracina* Linnaeus. Free-ranging, domesticated water buffalo (*Bubalus bubalis* Linnaeus) 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 tunneling and dung dwelling species in some of these natural pads. Small dwelling and tunneling 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 artificial dung pads (Barth et al., 1994; Lumaret & 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°C to 25°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 were at approximately 5:05 and 20:10, respectively. Moonrise on 09 June and 10 were 16:03 and 17:08, respectively, and moonset on June 10 and 11 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 min intervals, and at 5 to10 min intervals during peak ball production periods. The observers wore dark clothing and used low-powered torches to enhance visibility whilst minimizing potential disturbance of the subjects. Extreme care in the form of slow movements and hand-signaling was 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 1 kg 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 rhythm.

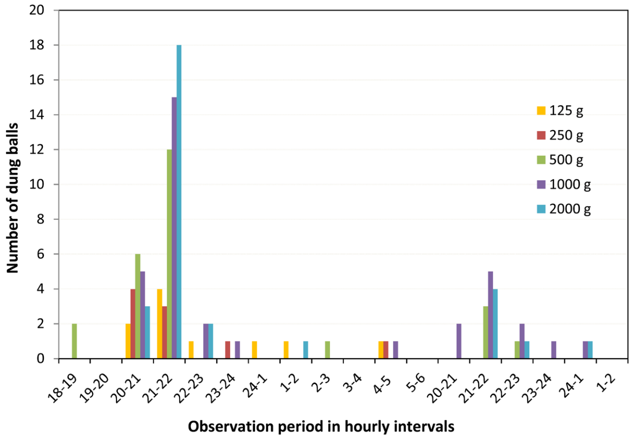

Fig. 1. Number of balls produced hourly for 48 h by *Scarabaeus sacer* L. from artificial dung pads on the Black Sea coast of Turkey (most hour periods during which no balls were produced are not included).

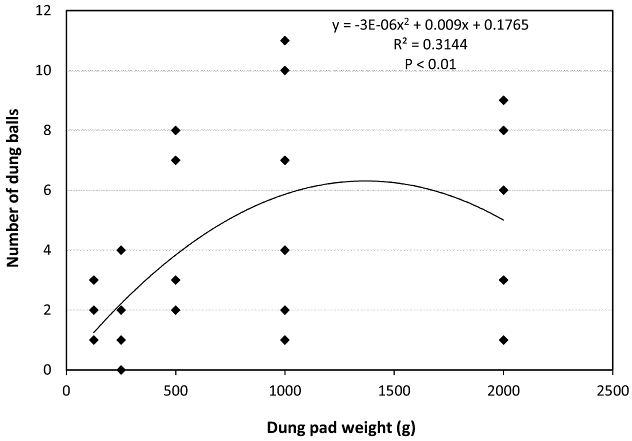

Fig. 2. Number of balls produced by *Scarabaeus sacer* L. in relation to size of artificial dung pads on the Black Sea coast of Turkey.

Statistical analysis

When data was not homogeneous, a square root transformation was applied before ANOVA. Duncan's Multiple Range Test was used to compare means 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.

RESULTS

Scarabaeus sacer produced balls from all 5 sizes of artificial 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 1, 2). Those 8 pads weighed 500 g, 1,000 g or 2,000 g and mean production was 8.3 balls/pad, compared with 1.4 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 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. 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).

Table 1. Number of balls produced by *Scarabaeus sacer* L. from five sizes of artificial dung pads on the Black Sea coast of 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 ($P < 0.05$).

For the 30 balls measured from the 5 pad sizes, volume ranged from 16 cc to 86 cc. Mean ball volumes for different pad weights were significantly different ($P < 0.05$) (Table 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 in 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 1, 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 ±

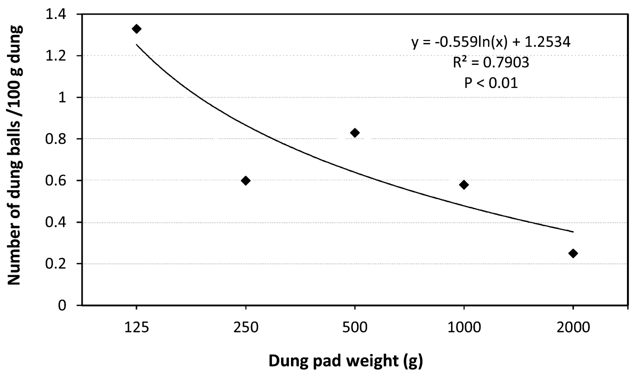

Fig. 3. Number of balls produced by *Scarabaeus sacer* L. per 100 g of dung in relation to size of artificial dung pads on the Black Sea coast of Turkey.

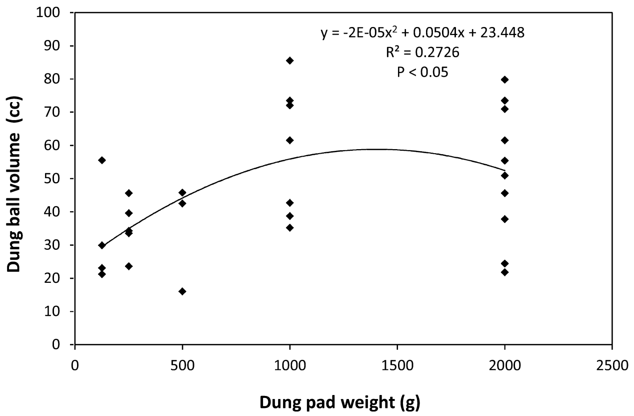

Fig. 4. Volume of balls produced by *Scarabaeus sacer* L. in relation to size of artificial dung pads on the Black Sea coast of Turkey.

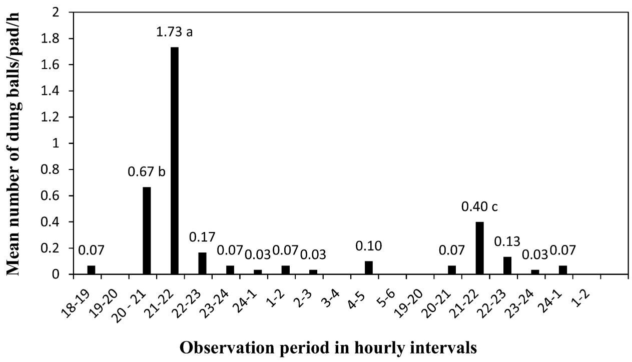

Fig. 5. Dung balls produced hourly over 48 h by *Scarabaeus sacer* L. from five sizes of artificial dung pad on the Black Sea coast of Turkey. Most hour periods during which no balls were produced are not included and means not labelled a, b or c are in group d. Different letters show a significant difference (P < 0.01).

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. By contrast, for both lines there was no significant difference in mean ball production/pad/hour between the middle replicate and the two end replicates.

DISCUSSION

Doube (1990) reported that rollers and large tunnelers 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 tunnelers. 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 & 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 1–2, Figs 1–4), 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 tunnelers 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. 2). Peck & 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.

Table 2. Volume of balls produced by *Scarabaeus sacer* L. from five sizes of artificial dung pads on the Black Sea coast of 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).

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 is probably a compromise between intraspecific competition and the probability of encountering potential mates. Furthermore, aggregation at the 8 pads would likely have reduced the 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 4). In comparison, Marsch (1982) reported that ball size ranged from 12 cc to 70 cc for *S. sacer*. Ybarrondo & Heinrich (1996) reported that competition at the dung pad reduces the size of balls. 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.

Scarabaeus sacer produced larger balls from larger pads, with the largest balls produced from 1,000 g pads (Fig. 4). The highest number of balls was also from the 1,000 g pads (Fig. 2) but ball production per 100 g of dung declined steeply as pad size increased (Fig. 3). The highest proportion of dung utilised was in 125 g pads (43%) and the lowest (13%), was in the 2,000 g pads. There was no clear pattern of use across the pad sizes, which further evidences the availability of sufficient dung to make a ball being more important than 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 reduced level of intraspecies competition.

Doube (1990) reported that most ball rollers remove dung within approximately 1 h 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 1, 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 & 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 2 studies (Figs 1, 5). Marsch (1982) and Verdú et al. (2004) reported the presence of *Scarabaeus semipunctatus* Fabricius and *Scarabaeus cicatricosus* (Lucas), respectively, which 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* is 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°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 and 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.

CONCLUSIONS

Artificial 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.

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