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Nesting behaviour, ontogeny and life-cycle of *Onthophagus stylocerus* (Coleoptera: Scarabaeidae)

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Abstract. Reproductive biology, nesting and ontogenetic development of *Onthophagus stylocerus* Gräells, 1851 are studied under laboratory conditions. The species is univoltine. Egg-laying begins at the end of May and lasts until July. The development from oviposition to imago takes 7–10 weeks. The aestivation of the offspring is combined with hibernation of emergent adults.

As with many other Onthophagini, sexual cooperation and food relocation for larval supply plays an important role in the nesting behaviour of *O. stylocerus*. Nest type may follow any of four patterns, involving: one or more entrance tunnels, branching and brood mass location. Pattern 1: simple, without branching; 1 to 5 brood-masses per nest; moderate depth: 60–160 mm. Pattern 2: simple, with branching but without brood masses in the stretch closest to the surface; 3–9 brood masses; depth: 100–315 mm. Pattern 3: simple, with branching, and brood masses in the stretch of tunnel closest to the surface; 6–7 brood masses; depth 130–220 mm, frequently 200–220 mm. Pattern 4: complex, with one or several entrance tunnels intersecting the main shaft at different levels or converging from the surface to the same brood mass; 10–14 brood masses; depth 280 mm.

Early spring emergence of *O. stylocerus* gives the larvae the time necessary to complete their development before the arrival of the Mediterranean mountain winter, and enables adults to avoid the severe competition which structures coprophagous communities in the late spring.

INTRODUCTION

The breeding-related activity of *Onthophagus stylocerus* Gräells, 1851 (Coleoptera: Scarabaeidae), native to central and north-western Spanish mountain ranges, is phenologically restricted (Bahillo de la Puebla, 1990; Galante, 1979; Galante & Rodríguez-Menéndez, 1989; Galante et al., 1988; Lobo, 1992; Martín-Piera, 1984; Martín-Piera et al., 1986). The demographic peak of *O. stylocerus* in central Spain occurs in the spring, ranging from 14 individuals per dung-pat in May to 12 in June. In May, it can make up as much as 25% of total dung-pat biomass (4.4 mg dry weight), decreasing to 4% in June (Lobo, 1992). Adults do not appear in other months of the year.

The main aims of the research have been the explanation of the seasonal appearance of the adults and the experimental study of its nesting behaviour in the evolutionary and ecological context proposed by Halffter & Edmonds (1982).

MATERIAL AND METHODS

Adults of *O. stylocerus* were captured 13 May, 1991 in pitfall traps baited with 1,000 g of fresh cow dung at an elevation of 1,650 m in Puerto de Cotos, near Madrid. This site is located at the oro-Mediterranean phytoclimatic range of the Ibero-Atlantic mountains in central Spain (Rivas-Martínez et al., 1987). At this altitude vegetation is a mosaic of mat-grasses, pines, and broom (*Cytisus purgans*). Climatically it is characterized by an annual average temperature of 6.4°C and an annual average rainfall of 1,170 mm. In June 1991, the average maximum temperaure was 19, and the minimum 8.8°C.

Eight beetles per cage (4♂ and 4♀) were put in four containers which consisted in two paralell plates of glass (43.5 x 16.5 cm) spaced 2 cm apart by frames of wood and held in position by clips (Klemperer, 1978). These cages could be opened rapidly and re-assembled with little disturbance to the beetles. A 38-cm layer of sieved, dampened, compacted humus from the capture site filled the cages. Fresh cow dung was supplied, and the cages kept darkened, dampened by periodic spraying with water from an atomiser.

Beetles were observed three times every week, and monitored while mating and building their nests. After 40 days, beetles were transferred to smaller cages (20 x 17 x 2 cm). This was made: i) to discriminate safely between parentals and offspring (F_1), ii) to avoid an excessive number of nests (tunnels and brood masses) which could block the building of new ones, and iii) to prevent aggressive behaviour between larvae, observed exceptionally when the brood masses were too contiguous. Only in the small cages 5 and 6 the transferred beetles were observed building new nests, but cage 6 housed only two couples due to beetle mortality (Table 1). Later, the offspring were also put in 3 additional large cages, and their behaviour observed. Larval behaviour and development were monitored directly, by opening carefully the brood-masses. The time of disturbance (white-light exposure – 60 W – and manipulation) was minimized; after each observation larvae were returned to their respective brood masses which were then closed carefully. They were repaired by larvae themselves. A total of 93 eggs, 88 first-instar larvae (LI), 83 LII, 72 LIII, 61 pupae, 59 teneral and 56 emerged adults were observed; this decrease was due to mortality (see Results).

Ontogeny and nesting behaviour were monitored in a rearing chamber with a 2-phase temperature control (see constants in Fig. 1); annual average temperature within chamber was: maximum 19.2°C, minimum 11.5°C. The temperature within cages was measured with a thermocouple connected to a thermometer. Temperature was less variable in cages than in the rearing chamber, reaching a maximum in the cages 4°C less than that of the chamber and a minimum 2°C greater.

RESULTS

Nesting

As in many other species of *Onthophagus*, males dug the brood nests, using their head and prothorax. Tunnel depth varied from 20 to 315 mm, but mostly from 90 to 200 mm, a range greater than in other species.

The number of brood masses built in each of the four big cages (1 to 4; Table 1) did not vary significantly (mean = 19.75 brood masses/cage; SD = 2.16; N = 13 nests), nor did it seem to be related with average depth (67 out of 93 – 72.04% – were at 50 to 160 mm). Nevertheless, brood masses variation increases when the six cages are considered: four large plus the two small ones (mean = 15.5; SD = 6.29; N = 18 nests). Cages 5 and 6 housed females which, presumably, were at the end of their reproductive period.

After having dug the tunnel, the male packed in bits of excrement. The female built the brood masses, and sometimes gathered excrement with the male; this collaboration was also observed in other species. The continual contact between the pair of beetles and in cooperation is a quite important stimulus for the nesting behaviour of mating couples.

As a check on the stimulating role of male-female cooperation, a parallel experiment was performed. Fourteen males and twenty females collected at the same mountain site, were distributed in two additional cages. After 21 days living together without any disturbance, females that presumably had mated were separated for 12 days. Nine days after having been reunited, beetles were observed to have built only one brood mass.

The layout and branching of tunnels, and brood-masses number, observed to be extremely variable, gave rise to the following classification:

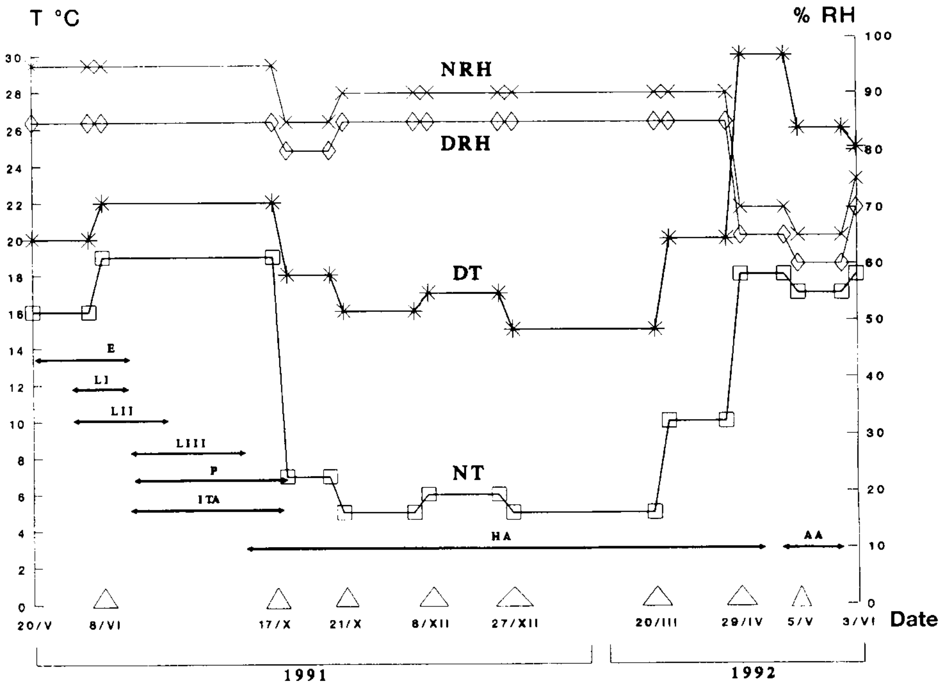

Fig. 1. Diagram of temperature and relative humidity in environmental rearing chamber *O. stylocerus*. NRH – night relative humidity; DRH – day relative humidity; DT – day temperature; NT – night temperature; E – egg; LI, LII and LIII – first, second and third larval instars; P – pupa; ITA – inactive teneral adults (recently emerged imagos aestivating in pupal chambers); HA – hibernating adults (imagos outside pupal chamber); AA – active adults (field observations).

Type 1. Simple with a single main entrance tunnel:

Type 1.1. Without branching (Fig. 2A). Contains 1–5 brood masses, with 1 or 2 most probable. It reaches moderate depth (60–160 mm, average 90–110 mm). Type 1.1 was found in 5 cages (Table 1).

Type 1.2. With branching but without brood masses in the stretch closest to the surface (Fig. 2B). Contains 3–9 brood masses, with 1, 2 or rarely, 6 in each of the three branches (depth 100–315 mm, commonly does not exceed 150–160 mm). Type 1.2 was found in 3 cages (Table 1).

Type 1.3. With branching, and brood masses in the stretch of tunnel closest to the surface (Fig. 2C), or else at the shallowest branching point. Contains 6 or 7 brood masses, with 1, 2 or 4 in each of the 2–5 branches (depth 130–220 mm, frequently 200–220 mm). In one case, there was a mass in the main tunnel, right at the intersection of two deeper galleries. (Fig. 2C; cell 2). Type 1.3 was found in 3 cages (Table 1).

Type 2. Complex, with several entrance tunnels (Figs 2D). Found in two cages, with only two variations. In the first (Fig. 3), the main shaft was intersected by two others that reached the surface, containing 2 and 4 brood masses, respectively; there were also two blind tunnels with 2 and 3 pedotrophic cells, respectively. The main tunnel contained another 3 (total 14 brood masses; depth of 220 mm). In the second (Fig. 2D), two tunnels, with 3 and 2 pedotrophic cells, converged from the surface to the same brood mass (number 4), from which there was another branch with 4 cells. Depth 280 mm. Type 2 was found in 2 cages (Table 1).

TABLE 1. Mating of *O. stylocerus* monitored in cages under environmental conditions shown in figure 1. Figures correspond to total nest types, brood masses, and emerged adults.

Cages		Nesting couples	Nest types (NT)				Brood masses and eggs (1 egg/brood mass)				Offspring: Imagos F_1			
Large	Small		1.1	1.2	1.3	2	(NT) 1.1	1.2	1.3	2	(NT) 1.1	1.2	1.3	2
1*		4♂, 4♀	2	1	1	–	3	9	7	–	1	5	6	–
2		4♂, 4♀	1	–	1	1	2	–	7	14	–	–	3	8
3		4♂, 4♀	–	–	–	2	–	–	–	20	–	–	–	12
4**		4♂, 4♀	1	2	1	–	2	9	6	–	–	6	3	
	5*	4♂, 4♀	2	1	–	–	3	3	–	–	2	3	–	–
	6**	2♂, 2♀	2	–	–	–	8	–	–	–	7	–	–	–
Subtotal		22♂, 22♀	8	4	3	3	18	21	20	34	10	14	12	20
Total		44	18				93				56			
							mean = 19.75; SD = 2.16[1]							
							mean = 15.50; SD = 6.29[2]							

Large cages: 43.5 × 16.5 × 2 cm

Small cages: 20 × 17 × 2 cm

[1] Brood masses/cage: Values calculated for cages 1 to 4 (16 mating couples; N = 13 nests).

[2] Brood masses/cage: Values caculated for the six cages (22 mating couples; N = 18 nests).

* Beetles transferred after 40 days from cage 1 to 5.

** Beetles transferred after 40 days from cage 4 to 6. Differences between cages 4 and 6 were due to beetle mortality.

Tunnels may be straight, curved, or frequently sinuous; brood masses are not always constructed in any apparently logical order, as occurs in simple nests without branching. New masses are sometimes built in the depths of a nest, below others built previously (Figs 2C and 3). Thus, brood masses do not impede the nesting adults from moving towards lower levels, as long as tunnels do not become obstructed by loose soil. In other

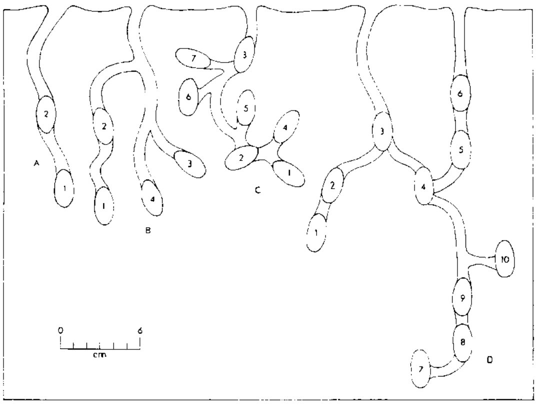

Fig. 2. Nest building types of *O. stylocerus*. Brood-mass building order indicated by numbers. A: Type 1.1. Simple nests, with two brood masses. B: Type 1.2. Simple branched nests, with four brood masses. C: Type 1.3. Simple branched nests, with seven brood masses. D: Type 2. Complex nest, with two entrance tunnels and 10 brood masses.

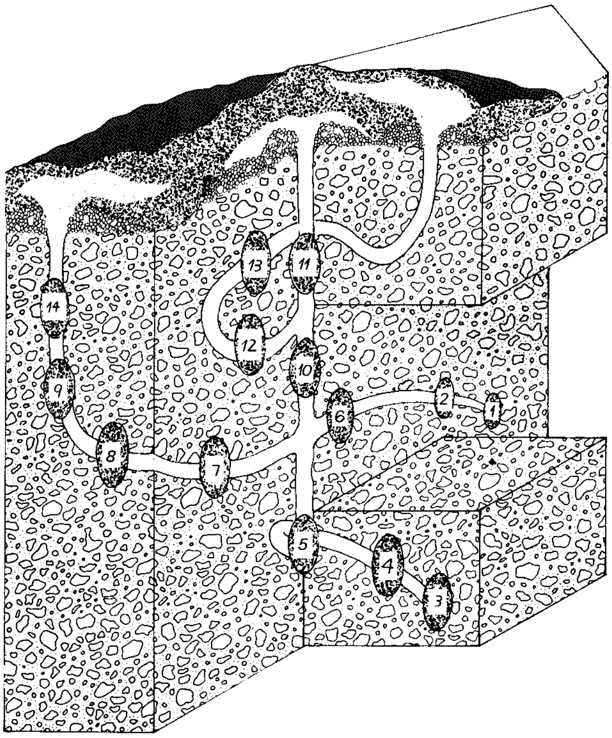

Fig. 3. Type 2. Complex nest, with three entrance tunnels and 14 brood masses.

nests, a couple of masses were built in the depths of the main tunnel, then a higher branch was completed, and finally, new masses were added to the former.

The construction of the nest terminates with the obstruction of the shafts between masses and the opening to the surface.

Brood masses

The brood mass (Fig. 4) consists of a compact nucleus of layers of excrement. Inside it is an oval chamber near the apical pole, with a clay cowl. In the chamber an egg is stuck to a piece of maternal dung, whose function is thought to be to inhibit possible growth of fungi (Halffter & Edmonds, 1982) and to enrich the excrement packed in the cell with the microorganisms (copro- and cellulo-symbionts) which help larval digestion: external rumen (Halffter, 1991).

Usually, brood masses are more or less egg-shaped, although they may be pear-shaped, spherical or sausage-shaped. Their weight, when fresh, averages 2.89 g. The number of masses per nest of *O. stylocerus* is rather similar to that of other European species of the genus. In the samples studied, the number varied from 1 to 14, and was related to the complexity of the nest. The average number of offspring (adults emerged) from twenty mating couples of *O. stylocerus* (cages 1 to 5 in Table 1) was 3.06 beetles/nest (N = 16 nests; SD

= 2.56), with an average of 5.31 masses/nest (SD = 3.77), yielding a juvenile mortality rate (57.6%) not necessarily representative of that in natural conditions (Table 2).

The female of *O. stylocerus* appears slow, taking 24 hours for construction of a mass. Brood mass age appears not to be correlated with the timing of adult emergence; adults do not necessarily appear first from the older cells, which is unsurprising if the variation in the 51–70 day cycle is taken into account.

Developmental stages (Fig. 1; Table 3)

EGG. Egg-laying began on May 22 and went on until July 23 (Fig. 1). The eggs measured 2.93 × 1.61 mm (N = 7), larger than in other species. The egg hatched after 5–10 days.

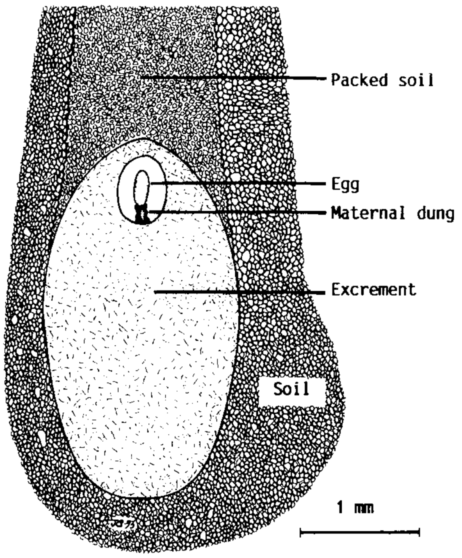

Fig. 4. Longitudinal cross-section of brood mass.

TABLE 2. Brood masses and offspring of 20 mating/nesting couples (N = 16 nests) of *O. stylocerus*. Cages 1 to 5, see Table 1.

No.	Cages	Nest types	Brood masses and eggs (1 egg/brood mass)	Offspring: Imagos F_1
1	1	1.1	1	–
2	1	1.1	2	1
3	2	1.1	2	–
4	4	1.1	2	–
5	5	1.1	1	1
6	5	1.1	2	1
7	1	1.2	9	5
8	4	1.2	4	1
9	4	1.2	5	5
10	5	1.2	3	3
11	1	1.3	7	6
12	2	1.3	7	3
13	4	1.3	6	3
14	2	2	14	8
15	3	2	10	5
16	3	2	10	7
Total			85	49
			mean = 5.31; SD = 3.77	mean = 3.06; SD = 2.56

LARVA. The newly-hatched larva began to feed toward the base pole, away from their oval chamber. In one case, a larva (second instar) was found to have not only advanced in the usual direction, but also to be devouring a neighbouring cell occupied by another recently-emerged larva (larva of cell 2 feeding on cell 4; Fig. 2C).

Larvae consume the greater part of the food supply in the mass during their first and second instars (LI and LII). When the supply is exhausted, the LII builds a spherical larval chamber with their excrement, which represents a large part of the contents of its gut, within the residual shell of what was the brood mass, and then undergoes a second ecdysis.

The first instar lasted 6–13 days, often 8–10; the second 10–15. The LII instar weight ranges from 0.10 to 0.34 g, with a growth rate of 0.01 g/day. While the larva moves freely within its brood mass, it is able to repair damage to the brood-mass wall with liquid faeces, manipulated with its legs and mandibles. After the second ecdysis, the third-instar larva (LIII) stays quiescent within its cocoon, reabsorbing the rest of the contents of its gut, reaching a weight of 0.37 g, that progressively lessens.

PUPA. Newly moulted pupa is entirely white and lies head down in the pupal chamber. With time, the cephalo-thoracic region acquires reddish hue and the shape of the adult. The elytra remain folded toward the latero-ventral side of the body.

The pupal stage lasted 11–17 days. Pupal weight was around 0.20 g, which decreased steadily until reaching the final adult live-weight: 0.10–0.18 g (mean = 0.11) in the male (N = 12), 0.06–0.12 g (mean = 0.10) in the female (N = 12). There was only one pupa whose last ecdysis occurred at the beginning of October.

TABLE 3. Size and duration of developmental stages of *O. stylocerus*.

Stage/instar	Weight (g)	N	Length (mm)	N	Duration (d)	N
Egg	–	–	2.93 x 1.61	7	5–10	93
Larva 1st instar	–	–	–	–	6–13	88
Larva 2nd instar	0.10–0.34	4	18.2–20.3*	2	10–15	83
Larva 3rd instar	0.37	2	22.56*	1	8–15	72
Pupa	0.2	1	11.26	1	11–17	61
Male	0.10–0.18 (av. 0.11)	12	9.9–12.5 (av. 11.2)	12	–	56
Female	0.6–0.12 (av. 0.10)	12	7.5–12.4 (av. 10.4)	12	–	

* Length = distance from cephalic capsule to abdominal hump + distance from abdominal hump to raster (Lumaret & Kim, 1989).

ADULT. Under laboratory conditions, such as those shown in Fig. 1, the juvenile adult remains for about 15 days inside the pupal chamber, as is the case with other species (*O. texanus*, for example). Afterwards, it emerges, but does not go up to the surface. With a duration often of 63 days, the cycle is comparatively long (see Table 4).

In periodically dampened cages, adult offspring aestivated from their emergence until September, staying underground without feeding (some until mid-September). From October on, this generation entered hibernation, interrupted only by occasional ascents to the surface to feed.

TABLE 4. Characteristics of the nesting patterns of species belonging to the genera *Onthophagus* and *Digitonthophagus*. Data from the literature: Lumaret & Kirk, 1987; Ohaus, 1909; Rougon & Rougon, 1980, 1991; Tyndale-Biscoe et al., 1981. Additional references in the text.

Nest spp.	Tunnel Depth (mm)	Brood mass Weight (g)	Brood mass Length (mm)	Brood mass Number/nest	Ontogeny Days
Digitonthophagus gazella	200–350	–	25 × 10	> 40	29.8
Onthophagus alluvius	25–203	–	12 × 7	20–40	35–52
O. batesi	–	–	11–16 × 9	–	–
O. binodis	0–200	–	–	–	–
O. browni	–	–	–	–	32
O. coenobita	250	–	–	5	–
O. compositus	100–200	–	–	4–6	–
O. dunningi	–	–	–	2–6	–
O. emarginatus	55	–	–	6	–
O. fracticornis	200	–	–	10	–
O. granulatus	–	–	–	70	–
O. hecate	51–229	–	17 × 8.5	–	–
O. incensus	101–203	–	–	–	–
O. lemur	120–300	–	–	13	–
O. maki	145	–	–	13	–
O. nuchicornis	160	–	–	7	–
O. medorensis	51–127	–	–	–	–
O. oklahomensis	25–51	–	10 × 8	–	21
O. ovatus	20–100	–	–	9–10	–
O. pennsylvanicus	51–76	–	10 × 6	–	21
O. striatulus	76–127	–	–	4	–
O. stylocerus	**20–125**	**2.89**	**25–38 × 13–18**	**1–14**	**51–70**
O. taurus	60–200	2–3.5	–	–	–
O. texanus	76–178	–	10–16 × 7–11	3–30	–
O. tuberculifrons	51–178	–	–	–	–
O. vacca	150–165	2–3.5	–	9	–

This occasional feeding activity was observed in the adults of both generations (offspring and parental). These laboratory observations lead to the hypothesis that, if temperature were the factor which triggers species activity, one could expect that by imitating such "spring weather conditions" in the laboratory, reproductive/nesting behaviour might be provoked, regard-less of the actual season.

To test this idea, two moistened cages (one with 2♂ and 5♀ from the parental generation, and another one with 3♂ and 5♀ offspring) were kept at a constant temperature of 22°C (daily temperature programmed in the rearing room from June to October) during the period December 13–19, 1991. This figure fits into the range of absolute maximum temperature recorded from May to June, 1991 at the Puerto de Cotos site: 19.7 (May) – 26.9 (June). Neither of the two generations began nesting, suggesting that the ovarial resorption was irreversible in the parental generation, and that the oocytes had not yet matured in the offspring. None of the remaining hibernating beetles, subjected to coldest weather conditions began nesting (Fig. 1).

DISCUSSION

Nesting behaviour

Nesting behavioural patterns and nest building features of *O. stylocerus* are similar to other *Onthophagus* species; however, some differences occur.

Males dug the brood nests, as is the case with many other species of *Onthophagus*, using head and prothorax (see Goidanich & Malan, 1964; Bornemissza, 1971a). The tunnel depth is greater than in other species (see Table 4). The continual contact and the cooperation between the sexes is quite important not only in gathering mass provisions but also because it appears to stimulate oviposition (Cook, 1988: *O. binodis*). A similar increase in fecundity has also been reported in *Phanaeus daphnis* Coprini (Halffter & López, 1977). Anduaga & Huerta (1983) have also found that isolated females of *Copris armatus* (Scarabaeinae: Coprini) began neither nest-building nor oviposition. In species adapted to consumption of pellets, such as *O. compositus* (Bornemissza, 1971b), collaboration is reduced to passing these pellets by the male to the female.

The layout and tunnel-branching patterns may be fitted in Pattern-I or Compound Type, as defined by Halffter & Edmonds (1982). Complex nests with several tunnels to the surface have been described by Burmeister (1936), Bornemissza (1970, 1971a,b) and Waterhouse (1974) in *Digitonthophagus gazella*. This is the most frequent type found in Onthophagini (Cambefort & Hanski, 1991). However, species which build a nest without branching are also known: *O. coenobita* (Burmeister, 1930). The number of masses per nest of *O. stylocerus* is rather similar to that of other European species, but the brood mass size is the greatest known in the genus. Outside of the Palaearctic, there is a tendency for the number of brood masses to increase (see Table 4). These figures may vary as a function of factors such as the soil water content and temperature (Barkhouse & Ridsdill-Smith, 1986; Tyndale-Biscoe & Walker, 1992), even to some extent, on the amount of dung readily available on the surface. The brood mass size ranges between 25–38 mm in length and 13–18 mm in width, with an average of 30 x 16 mm (N = 6; SD = 0.44 length x 0.22 width). The brood mass weight, when fresh, averages 2.89 g. By comparison, one of *O. taurus* or of *O. vacca* weights 2–3.5 g (Klemperer, 1981).

The mortality rate (57.6%) is rather similar to that in other species. According to Blume & Aga (1975), the average number of offspring from females of *D. gazella* is 16.5 indiv./10 days, even though they can lay up to 44 eggs in the same period. Mass construction by the female of *O. stylocerus* is slower than in other species, taking 24 hours. *D. gazella* can build one in two hours (Bornemissza, 1970), while *O. compositus*, a species which produces less elaborate brood masses, buries 4–6 kangaroo pellets per hour (Bornemissza, 1971b).

The egg size is larger than in other species (*O. alluvivus*, *O. texanus*, *O. medorensis* and *O. browni*; see Lindquist, 1935 and Howden & Cartwright, 1963). The eggs hatch after a longer period (5–10 days) than observed for *O. texanus* (2–4 days). The first, second and third-instar larva of *O. stylocerus* lasts a similar period to *O. texanus*, but pupal stage lasts 11–17 days, a longer than in that American species (5–7 days; see Howden & Cartwright, 1963).

The larva is able to repair mass-wall damage with liquid faeces, manipulated with its legs and mandibles. This repair technique has already been described in LII and LIII instars of other species: *Chironitis pamphilus* (Medvedev & Medvedev, 1958); *Bubas bison* and *B. bubalus* (Klemperer, 1981); *Onitis belial* and *O. ion* (Klemperer, 1982) and *Oniticellus cinctus* (Klemperer, 1983). The prepupae of *Bubas* lose 20% of their weight in these repairs. This behaviour has also been observed in *Geotrupes* sp. (Howden, 1955; Sano, 1915); *Ceratophyus gopherinus* (Ritcher & Duff, 1971) and *Peltotrupes chalibaeus* (Howden, 1952). Klemperer (1978) also described it in third-instar larva of *Geotrupes spiniger*, *Typhaeus typhoeus* and *Aphodius fossor*.

Although exceptional aggressive behaviour between larvae (second instar) hosted in contiguous brood masses was observed. This aggressive behaviour probably is due to a mere response to tactile stimuli of such an organism living in that confined conditions. However, as Klemperer (1981) points out, these attacks probably rarely occur under natural conditions.

With a duration often of 63 days, the cycle is comparatively long (see Table 4). However, environmental constraints can modify these figures from species to species. For example, mean egg adult development time in *O. australis* vary inversely with temperatures (Tyndale-Biscoe & Walker, 1992).

Life-cycle: An ecological perspective

It is probable that reproductive behaviour in cages under experimental conditions is not quite normal for dung beetles. Hence, it should not be assumed that laboratory results fit perfectly with behaviour in the field. Despite this, the nesting behaviour of *Onthophagus stylocerus*, as described above, fits into the Pattern-I or Compound nest type of Halffter & Edmonds (1982).

The nesting behaviour of *O. stylocerus* may be extremely variable, probably as much as those of many other *Onthophagus* species. To this date we know only of Type-2, or complex, Onthophagini nests (several tunnels to the surface) in *O. fracticornis*, *O. dunningi*, *O. granulatus*, *O. compositus*, *O. stylocerus* and *D. gazella* (Burmeister, 1936; Bornemissza, 1970, 1971a,b; Waterhouse, 1974). While common nesting behaviour traits may be an adaptive pattern of *Onthophagus* species, architectural features of nest types arise from the plastic behaviours of nesting couples. Little is known about the ecological and/or physiological causes of this behavioural plasticity, but we suggest that it may be due to competition for food and for space in the soil beneath the dropping (Cambefort & Hanski, 1991). Competition is commonly argued to be a major structuring force of dung beetles communities (Halffter & Edmonds, 1982; Hanski, 1991; Hanski & Cambefort, 1991, and references therein).

Complex type nests (Figs 2D and 3) could minimize the time and energy needed to provision a nest with the greatest possible number of brood masses, thus maximizing reproductive fitness (to compare nest types with offspring in Tables 1 and 2). In a simple nest, the mating pair takes dung from an epigeous chamber formed within the dung pat. The larger the number of brood masses, the greater the time and effort spent carrying food from an increasingly larger nest. More tunnel entrances allow a more rapid access to portions of still-intact dung. In this context, the ability to build complex nests may be a (perhaps facultative) successful response to inter- and intra-species competition for unpredictable and ephemeral resources, such as excrement (Hanski, 1991; Hanski & Cambefort, 1991). Of the coprophagous Iberian mountain species, *O. stylocerus* is the first to appear after the thaw. In this period, it makes up approximately 25% of the total biomass of the dung-beetle community. From such population abundance, inter- and intra-specific competition has been inferred by Lobo (1992).

Further experiments should be made to assess the importance of competition in the nesting behaviour of dung beetles couples. But, it should not be overlooked that over 40 days of nesting eight nesting couples (4 couples per cage) of *O. stylocerus* housed in two cages under the same conditions (cages 2 and 3), built complex nests. Four couples showed a rather equilibrated proportion of simple and branched nests (cages 1), and finally another four couples showed a tendency to increase the number of branched nests (cage 4). Females in cages 5 and 6 presumably were at the end of their reproductive period after forty days. However, in the cage 6, with only two nesting couples (instead of four) complex and branched nests was completely lacking (Table 1).

The Iberian species belonging to the genus *Onthophagus* appear to be univoltine with a demographic peak in the spring and another smaller in the autumn. The egg-laying period of *O. stylocerus* coincides with that observed by other authors for the emergence of this species in different places of the Iberian central system (Galante, 1979; Galante et al., 1988; Lobo, 1992; Martín-Piera, 1984). Unlike the case of many other species, there is no field evidence of autumn activity of *O. stylocerus* adults. Some autumn feeding activity was observed in the adults of both generations (offspring and parental) under laboratory conditions, but it is not biologically significant.

The fact that the activity of the *Onthophagus* species inhabiting mountains is markedly seasonal, suggests that the spring activity of post-diapause adults from dormancy in these species is under influence of temperature. Probably the emergence of *O. stylocerus* is activated by lower temperature than other Iberian *Onthophagus* species. *O. baraudi*, a markedly orophilous European species endemic to the Alps, is also active only in the spring (Lumaret & Stiernet, 1991). The emergence of North American *Onthophagus* species adults appears to be influenced by climatic factors (Howden & Cartwright, 1963).

The seasonal occurrence of coprophagous beetles varies regionally (Hanski, 1990). In the Gredos Massif, seasonal appearance of *O. stylocerus* is in accord with regional distribution; in May, abundance is greatest at lower elevations; in July, populations are more numerous above 1,700 m (Lobo, 1992). Therefore, field and laboratory data suggest that the early spring emergence of *O. stylocerus* populations is an adaptative response to both regional and seasonal weather variations which gives *O. stylocerus* larvae the time necessary to complete their development before the arrival of the severe Mediterranean mountain winter. Furthermore, the early spring occurrence of adults would also be a good strategy to cope with the ecological constraints determined by the severe competition arising from the orophilous insect coprophagous communities in the late spring (Lobo, 1992).

O. stylocerus also colonizes Atlantic Spain in Galicia, País Vasco and León, where the phenology of all captures was that of central system mountains. As *O. stylocerus* spatially modifies its seasonal appearance, a study of the behaviour of these Atlantic populations in the field and/or laboratory might provide interesting comparisons.

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