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AN ECOLOGICAL STUDY OF THE DUNG BEETLE

Bubas bubalus (Oliver, 1811) *(Col. Scarabaeidae)*

Carlos J. Lumbreras, Eduardo Galante and Javier Mena

Unidad de Zoología. Facultad de Biología

Universidad de Salamanca. 37071 Salamanca (España)

RESUMEN

Se realizó un seguimiento directo de la actividad de los individuos de *Bubas bubalus* (Oliver, 1811) en encinares mediterráneos del oeste de la Península Ibérica. A la vez se recogieron nembras para análisis del desarrollo ovárico, desgaste de las tibias, acumulación de cuerpo graso e inseminación.

El ciclo de vida de esta especie se completa en el transcurso de un año presentando dos náximos poblacionales coincidentes con picos de emergencia de adultos. Existe una clara elación entre el desarrollo de la ovariola y el comportamiento reproductor. Este coprófago es ípicamente crepuscular con el máximo de actividad de vuelo situado en un corto intervalo de uminosidad (70 y 20 lux). Las cópulas se producen desde los primeros momentos de la mergencia del imago, no habiendo relación entre el grado de desarrollo de la gónada y la resencia o ausencia de espermatozoides en la espermateca. Desde la emergencia hasta la idificación pasan por una etapa de activa alimentación con el consiguiente acúmulo de cuerpo raso. Las puestas se realizan en masas de estiércol de 65 gr y 35 ml por término medio, nterradas a una profundidad variable entre 8 y 35 cm . El estudio bajo condiciones de campo vela una mínima contribución de los machos en la construcción y preparación de los nidos.

ABSTRACT

The activity of *Bubas bubalus* (Oliver, 1811) was studied in Mediterranean holm-oak wooded areas ("dehesas") in the west of the Iberian Peninsula. At the same time females were collected for analysing ovary development, tibial wear, accumulations fat-body and insemination.

The life cycle of this species is completed during the course of a single year, with two population maxima coinciding with the peaks of adult emergence. There is a clear relationship between ovariole development and reproductive behaviour. This dung beetle is typically crepuscular with maximum flight activity during a short interval of light intensity (70 and 20 lux). Copulation occurs immediately after the emergence of the adult; no relationship was found between the degree of gonad development and the presence or absence of spermatozoids in the spermatheca. Between emergence and nesting there is a period of intense feeding with the consequent accumulation of fat-body. The eggs are laid in brood masses (on average 65 g. and 35 ml.), at a depth which varies between 8 and 35 cm. A study made under field conditions revealed a minimal contribution of the males towards the construction and preparation of the nests.

KEY WORDS: *Scarabaeidae*, dung beetle, ecology, temporal activity.

INTRODUCTION

Following the studies of Halffter & Matthews (1966) and Halffter (1977) on the different nesting patterns in the subfamily *Scarabaeinae*, considerable attention has been paid to the study of ovarian development and its relationship with reproductive behaviour. Likewise, the study of changes occuring in the ovaries (Detinova, 1962), signs of copulation (Usinger, 1966), somatic changes such as fat-body cycles (Waloff,1958) or external modifications such as tibial wear (Tyndale-Biscoe, 1978), provide information which is in themselves or by combination valuable for detailed analyses of the insect populations (Tyndale-Biscoe, 1984).

Studies of the spatio-temporal distribution of the different species complement our knowledge of their ecology. Thus, besides biogeographical and phenological knowledge, the study of daily flight activity plays an important part in this ecology. The importance of this activity in insects is demonstrated by the extensive list of existing publications in the bibliography (see Saunders, 1982).

In the present study, we studied the ecology of one of the species, *Bubas bubalus* (Oliver, 1811). This species has, because of its biomass and activity during most of the year, one of the greatest potentials for the decomposition of dung in the mediterranean wooded areas, and thus contributes towards recycling organic matter in these areas.

MATERIAL AND METHODS

Experimental sites. During 1986, 1987 and 1988 monthly samples were taken on two experimental cattle farms ("Castro Enríquez" and "Campillo") in the province of Salamanca (Spain). The straight line distance between both farms is 14 Km; cattle, sheep and swine graze here throughout the year. The climate in both areas is of the extreme continental type with great variations in temperature: winters are cold, summers are hot and dry. The climax vegetation is the Mediterranean holm-oak area, with a dominance of *Quercus rotundifolia* Lam. Due to antropozoogene activity, the vegetation in both farms consists of clear-felled, savanna-like woodland ("dehesas") alternating with open pasture. At "Castro Enríquez", these pastures have neither trees nor shrubs (Fig.1), whereas at "Campillo" there is a greater variety of habitats, including wooded pasture, with and without underbrush, as well as open pasture, with and without underbrush (Fig. 2).

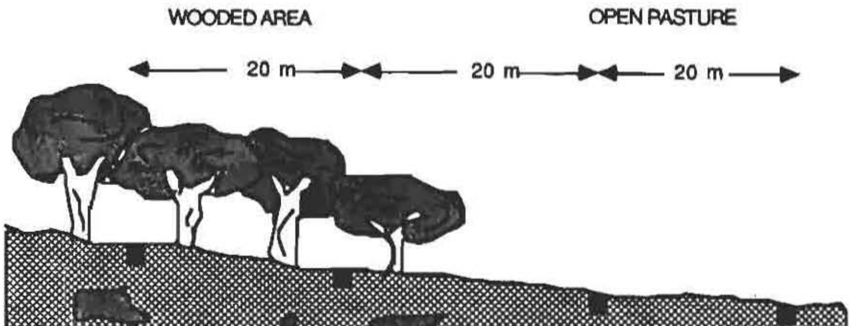

Fig.1. Schematic representation of habitats (wooded area and open pasture) and location of pitfall traps ■ at "Castro Enríquez" (40° 52' N and 6° 3' W; average altitude of 803 m a.s.l)

Activity.- We used from pitfall traps, following the model described by Hanski (1980), during the period April 1987-March 1988. This type of trap has the advantage that it is not selective with regard to the species captured (Lobo, Martin-Piera & Veiga, 1988). Eight of these traps were arranged in 2 parallel rows (4+4= duplicate), with half of the traps located in the wooded area and the other half in the open pasture (Fig.1). The main study area was "Castro Enríquez", while additional samplings were taken at "Campillo" to complement these results. The presence of habitats with underbrush was taken into account when choosing positions for the traps on the second farm (Fig. 2).

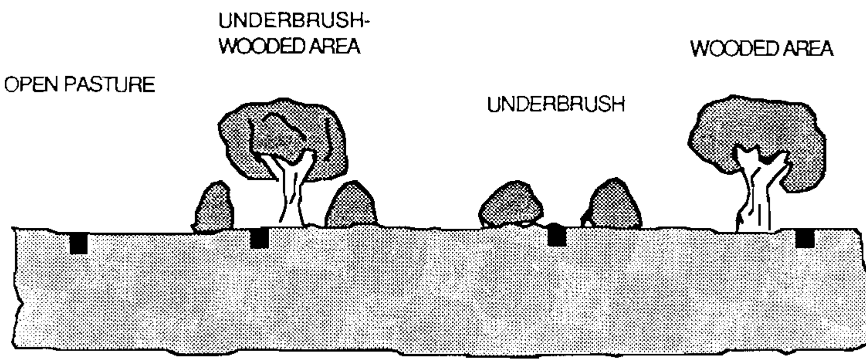

Fig.2. Schematic representation of the diversity of habitats (open pasture, underbrush-wooded area, underbrush and wooded area) and location of the pit-fall traps ■ at "Campillo" (41°0' N and 6°3' W; average altitude of 805 m a.s.l.)

As a bait we placed 900 cc of fresh cattle faeçes, with an approximate weight of 1150 g. The preserving fluid used was 200ml/trap of 50% ethylene-glycol. The complete contents of each trap were collected after each established period and replaced by fresh bait and fluid.

The monthly samplings were taken over a period of 48 hours, each 24 hours being divided into 4 periods whose length varied according to the season of the year (Table 2). Daily flight activity was estimated basically by direct observation of the traps. The interval of daylight during which activity was recorded was established by use of a Panlux electronic 2 photometer with 0 to 200.000

lux sensitivity. The data obtained, allowed establishing of seasonal and daily activity of the beetles (Fig. 3).

Dissections.- In order to analyse the condition of the tibias, accumulations of fat-body, ovary development and insemination, females were collected every month from November 1987 to December1988. These were placed in breeding containers with a little earth and fresh faeces to keep them alive until reaching the laboratory. The beetles were killed in 98% ethyl acetate and dissected in a 0.9% saline solution following the methodology of Tyndale-Biscoe (1978).

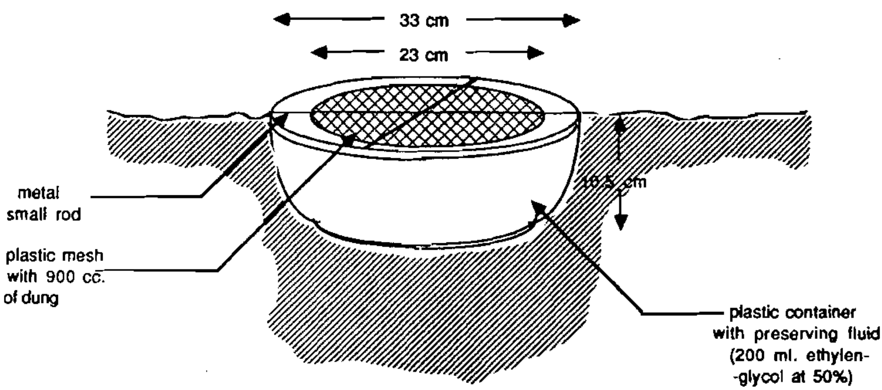

Fig.3. Details of the pit-fall used for following *Bubas bubalus* activity.

Five grades of tibial wear were considered, from grade 0 (no wear) to grade 4 (tibial teeth worn down level and absence of claws) (Fig. 4). Fat-body contents were classified from lesser to greater abundance in five categories (from 0 to 4). The ovariole was placed on a slide under a dissecting microscope, in order to examine its degree of maturity. The maximum and minimum diameters of the terminal and subterminal ovules were measured with a fitted micrometric eyepiece. These and the remaining small ovocytes measuring $\geq$1 mm. were counted. As the cross section of the ovules is usually elliptic, more or less elongated in the different phases of the ovarian cycle, their volume was calculated by the formula for a revolution ellipsoid:

$$V = 4/3\,\pi\,(a/2)\,(b/2)^2$$

where "a" = length of major axis (maximum length) in mm. and "b" = length of minor axis (maximum width) in mm. The spermatheca was then separated and squeezed under a coverslip to see if it contained spermatozoids and lence, to establish whether or not copulation had taken place.

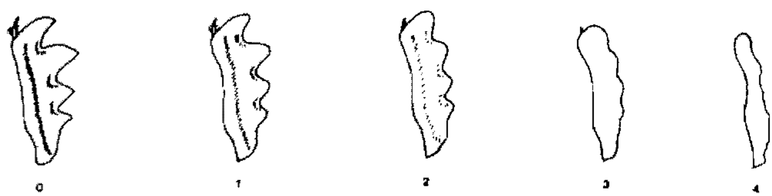

Fig.4. Different categories of tibial wear in females of *Bubas bubalus*: from unusued (0) to maximum wear (4).

Nests.- Our third objective in taking these samplings, was to obtain data on the nests of this species. Were measured the maximum and minimum diameters of the faeces, counted the number of surface holes, and measured their depths. The accumulated dung was taken out of four holes (Table 9), for establishing their weight and calculating its volume. In each case, it was examined for the presence of adults, eggs and /or larvae.

Weather recordings.-The data concerning rainfall and temperature were taken at a meteorological station (Cubo de Don Sancho, Salamanca) at 21 km. from the experimental sites (Table 1).

RESULTS AND DISCUSSION

Activity of *Bubas bubalus* (Ol.).

Seasonal activity patterns.- In the study area, *Bubas bubalus* is a univoltine species exhibiting activity throughout most of the year (Fig. 5a). According to

Table 1

Climatological recordings from April 1987 to December 1988 at the meteorological station in Cubo de Don Sancho, at 21 km. from the study sites. Rainfall corresponds to the total of mm recorded in each month. Temperatures are expressed as monthly means: Mean temperature af daily maxima (max.), mean temperature of daily minima (min.) and mean temperature of daily means (mean).

Month examined	Rainfall in mm	Median temperature (°C) max	min	mean
Apr 87	97.1	15.25	5.83	10.54
May 87	27.8	19.69	6.09	12.89
Jun 87	20.2	25.53	10.80	18.165
Jul 87	51.6	28.56	14.00	21.28
Aug 87	25.0	31.20	14.22	22.71
Sep 87	65.1	28.10	13.90	21.00
Oct 87	113.1	14.40	7.60	11.00
Nov 87	24.4	12.40	2.80	7.60
Dec 87	56.7	9.30	3.30	6.30
Jan 88	96.8	7.70	2.20	4.95
Feb 88	44.1	10.6	-0.20	5.20
Mar 88	4.40	14.8	-0.10	7.35
Apr 88	99.6	14.6	4.70	9.65
May 88	81.6	17.8	7.10	12.45
Jun 88	91.4	22.2	9.30	15.75
Jul 88	62.1	27.29	11.13	19.21
Aug 88	0.00	31.10	10.30	20.7
Sep 88	5.00	28.67	15.83	22.25
Oct 88	63.2	19.10	6.35	12.72
Nov 88	55.8	15.63	2.92	9.27
Dec 88	0.00	8.74	-2.19	3.27

the data obtained, temperature and rainfall are two important meteorological factors that determine the emergence of the adults. Surface activity ceases during the summer months; during the winter it is considerably reduced as a consequence of the adverse weather conditions. Greater abundance was detected in autumn and especially in spring. The first peak of abundance appears during the months of October and November, after the autumn rainfall. The second peak is detected later on, in March, coinciding with the milder spring temperatures and rain. Thereafter,with the arrival of the hot, dry summer period a progressive decline begins. Other studies (Galante, 1979; Paulian et Lumaret,1972; Lumaret,1978) suggest only one maximum, during spring, with the appearance of adults in February or March, depending on the area. The absence of an autumn peak in these studies is related to the drought that ocurred in this season during their study period. This circumstance did not occur during the autumn corresponding to the present study, and thus a population peak was observed at this time.

Table 2

Trap catches of *Bubas bubalus* at "Castro Enríquez" and "Campillo" during 1987 and 1988.

Habitats at Castro Enríquez								
Month of trapping	OPEN PASTURE				WOODED PASTURE			
	Mo	Af	Ev	Ni	Mo	Af	Ev	Ni
Apr 87	-	2	18	3	-	1	4	2
May 87	-	1	1	5	-	-	1	19
Jun 87	-	-	8	10	-	-	1	12
Jul 87	-	-	-	-	-	-	-	-
Aug 87	-	-	-	-	-	-	-	-
Sep 87	-	-	-	-	-	-	-	-
Oct 87	-	6	25	1	-	-	10	-
Nov 87	-	1	-	-	-	-	-	-
Dec 87	-	-	8	-	-	1	2	-
Jan 88	-	-	-	1	-	-	-	-
Feb 88	-	1	-	1	-	-	-	-
Mar 88	-	2	-	6	-	-	-	7

Habitats at Campillo																
Month of trapping	Open pasture				Underbrush-wood.Area.				Underbrush				Wooded Area.			
	Mo	Af	Ev	Ni	Mo	Af	Ev	Ni	Mo	Af	Ev	Ni	Mo	Af	Ev	Ni
Jun 88	-	1	2	-	-	-	1	2	-	1	1	3	-	1	1	3
Jul 88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aug 88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oct 88	-	-	5	-	-	-	1	-	-	-	5	-	-	-	4	-

	Mo: Morning	Af: Afternoon	Ev: Evening	Ni: Night
Spring	5.30-10.30	10.30-16.30	16.30-19.30	19.30-5.30
Summer	5.00-11.00	11.00-17.00	17.00-20.00	20.00-5.00
Autumn	7.00-12.00	12.00-16.00	16.00-18.00	18.00-7.00

(Expressed in solar time)

The species tended to occupy open areas with or without underbrush (31% of the total number of specimens caught were found in the latter area) (table 2). When temperatures start to increase (from April onwards) the presence of specimens in the wooded area is higher than in the open pastures (Fig. 5b &

c.). The increase in temperature presumably causes them to concentrate in the wooded zone, where environmental conditions are milder (lower temperature, greater environmental and substrate humidity). These movements can be related to "trivial range" (Southwood, 1977), "limited area range" (Baker,1978) or"behavioural range" (Hanski, 1980), which are a result of changes in habitat conditions, or a response to feeding habits.

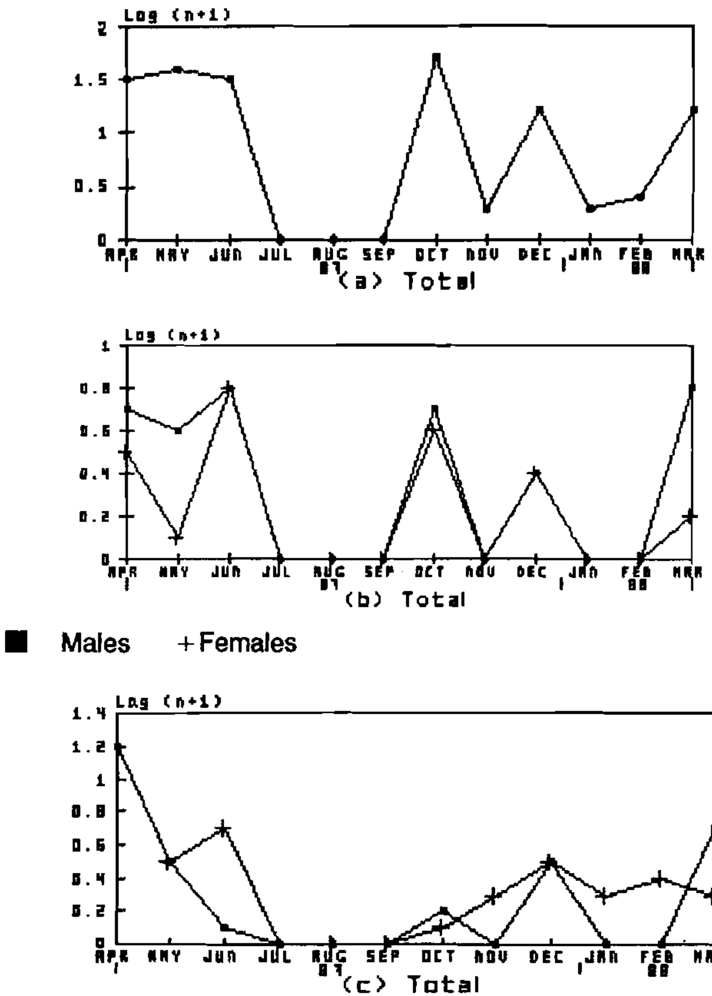

Fig.5. Seasonal activity of adult Bubas bubalus at "Castro Enríquez" from April 1987 to March 1988: (a) total number of beetles caught in traps; (b) trap catches of males and females in a wooded area and (c) in open pasture. n = monthly number of individuals caught in traps.

By examining the tibial wear it is possible to distinguish among age groups, ranging from newly-emerged young to the oldest individuals during the egg-laying and nesting period. This allows us to follow the aging process of the *B. bubalus* population in the study area (Fig. 6). The mean grade of tibial wear per month increased steadily from November 1987 (0.49) until June (3.00) and July (2.89) 1988. The same tendency was observed at the beginning of a new generation (Table 3).

Table 3

Tibial wear in females of *Bubas bubalus* collected in the Salamanca area.

0 = tibias without wear to 4 = tibias totally worm.

m.N. = mid-November; f.N. = end of November.

	Tibial wear of females				
Month of examined	0	1	2	3	4
Nov 87	28	27	-	-	-
Dec 87	3	10	-	-	-
Feb 88	2	13	-	-	-
Mar 88	25	16	2	-	-
Apr 88	2	10	20	2	-
May 88	2	7	7	4	2
Jun 88	1	-	4	5	7
Jul 88	-	-	5	11	3
Oct 88	10	8	-	-	-
m.N. 88	3	35	-	-	-
f.N 88	1	19	-	-	-
Dec 88	1	17	-	-	-

The teeth on the tibias of newly emerged females are well pointed (wear = 0). These were caught mainly in November 1987 and March 1988, and also in October and at the beginning of November 1988, with the start of a new cycle. This suggests that *Bubas bubalus* has two peaks for the emergence of adults (two minimums of tibial wear) associated with the autumn and spring population maxima (Fig. 5a). Furthermore, the females trapped during these periods of emergence had, in contrast to those caught in the other months, numerous intact bristles in the ventral area and a soft, shiny cuticle. It is interesting to note that mites were absent on the young individuals, in contrast to the oldest females, which harbour mites in their ventral regions.

As a result of their digging activity, the young females gradually wear away their tibias until the teeth become blunt (wear = 1,2 and 3). This continues (Fig. 6) until a maximum degree of deterioration is reached in June and July, when, in extreme cases, no vestige of teeth can be observed (wear = 4). This is typical for specimens caught during advanced nesting activity, which has caused greater wear.This maximum degree of wear coincides with a decline in the numbers of specimens during June and July.

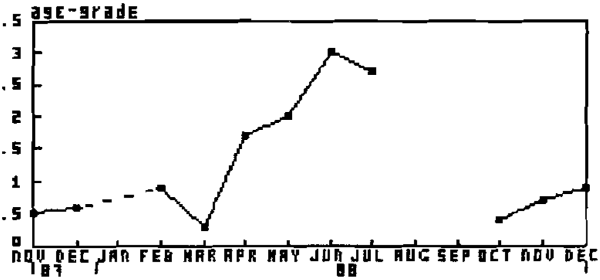

Fig.6. Evolution of the monthly average of age-grade of *Bubas bubalus* females, based on tibial wear. Due to the difficulty of catching individuals during January, the discontinuous line represents their assumed evolution. m.N = mid-November; f.N. = end of November.

The grade of tibial wear is at any time an excellent indication of the age of the population. As Edwards (1986) has reported for *Onitis caffer* Boheman, the gradually increasing age structure confirms that a period of continuous growth and consequent ageing of the population follows the emergence period.

Examination of the condition of the males tibias revealed that, on the whole, the grade of wear was minimal (0 and 1, at most 2, on rare occasions). This suggests that the males perform little digging activity in comparison to the females, and consequently their contribution to nest construction is presumably minimal.

Daily flight activity.- The flight period is the result of the interaction between an endogenous circadian rhythm, already described in other scarabaeidae (e.g. Geisler, 1961; Houston & McIntyre, 1985; Warnecke, 1966; Wensler, 1974) and environmental factors, especially light intensity (e.g. Aschoff, 1960;1965; Dreisig, 1980; Margalef, 1974). The daily flight activity of *Bubas bubalus* is restricted to the last hours of daylight, when light intensity is low but not nonexistent: from 110 to 0 lux. The maximum number of captures (85 to 90% of the total observed) was made during a short time interval (10 to 15 minutes) during which light intensity is between 70 and 20 lux (Table 4).

Table 4

Photometric recordings taken at "Campillo" during the periods of maximum activity of *Bubas bubalus* (autumn and spring).

	Illumination level	
Date of observation	110 - 0 lux	0 lux
Autumn 1988	10 m. 16 f.	0 m. 1 f.
Spring 1989	33 m. 46 f.	2 m. 3 f.

f = adult females m = adult males

Use of the photometric device allowed to establish that it was during this period that *Bubas bubalus* is active. As Mena, Galante & Lumbreras (in preparation) point out, the use of traps poses problems in the differentiation between crepuscular and nocturnal species. A crepuscular species is active during the last 10-15 minutes of natural light, but as a consequence of the number of traps and the distance between them, the period of collection and replacement is 35-40 minutes. This implies that results for the last traps do not attribute activity to the correct period (evening), but to the following night. Thus, in our study area *Bubas bubalus* is a crepuscular species, in contrast to other studies (Avila & Pascual, 1988; Lumaret & Kirk, 1987) in which complementary methodology (photometer) was not used and the flight activity of this species was not accurately recorded.

Ovary development and Insemination.

Gonad development in females. Bubas bubalus shows an extreme reduction in the female reproductive system. There is only one ovary with one ovariole, as in the other species of the *Scarabaeidae* family studied (Halffter & Matthews, 1966; Richter & Baker, 1974).

Ovariole development is fast, as is quantitively demonstrated in two aspects: the appearance of both a greater number and a greater volume of oocytes in vitelogenesis. Throughout the life cycle, the number of oocytes that matured varied between zero and a maximum of nine or ten. Most typically there were three or four (Fig. 7). The fact that in March both extreme values appear (0 and 9-10 oocytes), confirms the correspondence between the two population maxima and the two peaks in the emergence of adults: one during October-November, and the other in March. Thus females that emerged in autumn are found in March with a fully differentiated ovary (up to 10 oocytes). During March there also appear females in the initial stages of development; their ovary is not yet differentiated (0 oocytes) and they correspond to those that emerged in spring from the latest ovipositions of the previous year.

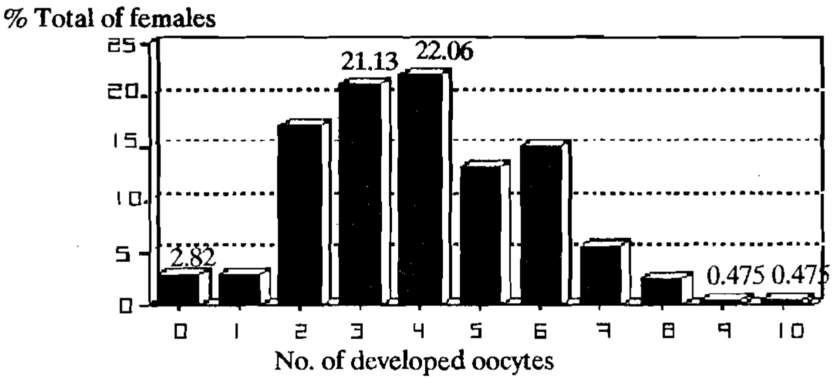

Fig.7. Number of oocytes larger than 1 mm appearing in the ovarioles of the *Bubas bubalus* females, from November 1987 until July 1988.

Table 5 shows that females with oocytes $\leq$ 1 mm in their ovary (0 oocytes) are found only during November and March. During March appear females with a maximum of up to nine or ten oocytes. The existence, in November, of females with undeveloped oocytes indicates that this is a period of adult emergence.

Table 5

Monthly percentage of *Bubas bubalus* females according to the number of oocytes developed.

Month of	No of oocytes larger than 1 mm									
examined	0	1	2	3	4	5	6	7	8	9	10
Nov 87	1.82	3.65	16.36	29.09	14.54	12.73	14.54	5.45	1.82	-	-
Dec 87	-	-	23.08	15.38	38.47	7.69	15.38	-	-	-	-
Feb 88	-	-	6.67	20	13.33	20	33.33	6.67	-	-	-
Mar 88	11.63	2.33	27.91	13.95	6.97	4.64	16.28	9.30	2.33	2.33	2.33
Apr 88	-	-	-	18.18	39.39	27.28	9.09	3.03	3.03	-	-
May 88	-	-	4.55	27.27	36.35	13.64	9.09	4.55	4.55	-	-
Jun 88	-	15.38	-	15.38	38.46	7.70	15.38	-	7.70	-	-
Jul 88	-	5.26	36.84	21.06	15.79	10.53	5.26	5.26	-	-	-

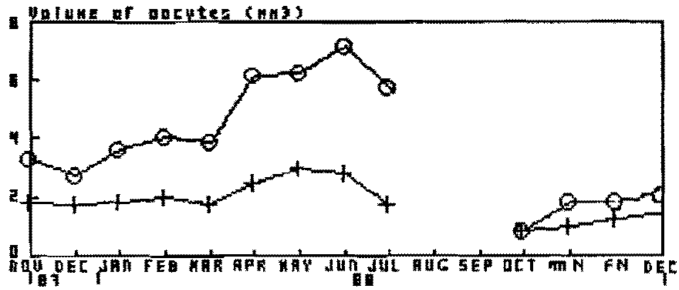

Fig.8. Gonadal cycle of female *Bubas bubalus:* Evolution of terminal (O) and subterminal (+) oocytes throughout the activity period. Due to the difficulty in catching individuals during January, the discontinuous line represents the assumed increase. m.n = mid-November; f.N = end of November.

Ovary differentiation was also evident from the greater volume of the oocytes. The volumes of terminal and subterminal oocytes calculated for each month are summarised in Table 5, thus obtaining the gonadal cycle reflected in Fig. 8. There is a parallel, progressive increase in the volume of both types of oocytes. Their growth begins around November, coinciding with the emergence of the first individuals, and continues without interruption until June, in the case of the terminal oocyte, or May for the subterminal oocyte. This progression was particularly patent after March, when it increased from 4.38 mm^3 in February and 4.33 mm^3 in March, in the case of the terminal oocytes, and 1.79 and 1.72 mm^3 respectively, for the subterminal oocyte, to almost twice these figures in April (6.51 and 2.47 mm^3). However, it should be noted that punctually in December and March a decline occurred, which in both cases can be explained by the large amount of egg resorption that took place (m.s. in preparation). It should also be taken into account that, especially during March, new individuals were emerging, so that the oocytes of some females were in the initial stage of development (this can be seen in the similarity between the figures for November and those for March). However, the differences between both types of development can be explained in terms of a differential growth is in both oocytes. Initially, growth progresses in favour of the terminal oocyte and subsequently in favour of the subterminal oocyte. Such a sequential maturation implies that the terminal oocyte is prepared or almost prepared for laying at the appropriate moment (Tyndale-Biscoe, 1978).

When development has been completed, a regression phase begins which corresponds to the end of the nesting period. This continues until the appearance of the new generation, following the process of larval development (basically from July to September).

Table 6

Biometry of the oocytes of the *Bubas bubalus* females. For both oocytes the first and second figure separated by * corresponds to the monthly average of maximum length and width expressed in mm. m.N = mid-November; f.N = end of November

Month of dis sected	Terminal oocyte	Subterminal oocyte	Volumes (mm^3) Terminal		Volumes (mm^3) Subterminal	
	mean ± sd * mean ± sd	mean ± sd * mean ± sd	mean ±sd	n	mean ± sd	n
Nov 87	2.04 ± 0.71 * 1.57 ± 0.44	1.50 ± 0.41 * 1.27 ± 0.38	3.26 ±2.79	54	1.58 ± 1.64	54
Dec 87	1.88 ± 0.66 * 1.54 ± 0.45	1.49 ± 0.43 * 1.28 ± 0.33	2.94 ± 2.69	13	1.52 ± 1.20	12
Feb 88	2.15 ± 0.61 * 1.82 ± 0.46	1.61 ± 0.35 * 1.37 ± 0.32	4.38 ± 3.07	15	1.79 ± 1.12	15
Mar 88	2.13 ± 1.06 * 1.66 ± 0.57	1.56 ± 0.66 * 1.23 ± 0.44	4.33 ± 4.92	39	1.72 ± 1.84	39
Apr 88	2.89 ± 0.80 * 2.00 ± 0.41	1.82 ± 0.44 * 1.51 ± 0.34	6.51 ± 3.44	33	2.47 ± 1.61	33
May 88	2.81 ± 0.72 * 2.05 ± 0.42	1.87 ± 0.62 * 1.52 ± 0.46	6.87 ± 4.37	22	2.88 ± 2.40	22
Jun 88	2.73 ± 1.01 * 2.09 ± 0.46	1.81 ± 0.91 * 1.45 ± 0.49	7.29 ± 5.58	16	2.78 ± 3.61	13
Jul 88	2.55 ± 0.62 * 2.05 ± 0.49	1.54 ± 0.39 * 1.29 ± 0.32	6.48 ± 5.31	19	1.53 ± 1.06	18
Oct 88	1.10 ± 0.24 * 0.90 ± 0.14	0.86 ± 0.18 * 0.68 ± 0.15	0.49 ± 0.24	18	0.23 ± 0.14	18
m.N 88	1.54 ± 0.49 * 1.21 ± 0.41	1.15 ± 0.28 * 0.94 ± 0.29	1.55 ± 1.87	38	0.65 ± 0.61	38
f.N 88	1.53 ± 0.36 * 1.31 ± 0.26	1.23 ± 0.19 * 1.00 ± 0.23	1.53 ± 0.95	19	0.70 ± 0.38	19
Dec 88	1.51 ± 0.51 * 1.26 ± 0.32	1.19 ± 0.46 * 0.99 ± 0.32	1.56 ± 1.80	18	0.82 ± 1.15	18

The volumes calculated at the end of October, middle and end of November and December 1988 provided evidence concerning the beginning of the new generation of the next year (Table 6).

Insemination. Analysis of the spermatheca indicated that 80% to 100% of the females dissected each month were inseminated (Table 7).

These high percentages indicate that copulation must have taken place from the first moments of life of the adults. The occurence or not of insemination was associated with both immature and mature ovaries, spermatozoids being observed shortly after emergence of the adults when the ovary was undeveloped. Once the ovaries were fully developed, all the females showed spermatozoids in their spermathecas, the month of July being an exception (95 %) when one female was found that was not inseminated despite an advanced stage of ovary development.

Table 7

Monthly percentage of insemination in *Bubas bubalus* females: abscence (0) and presence (+) of spermatozoids in the spermateca.

Month of dissected	% of insemination	
	0	+
Nov 87	10.91	89.09
Dec 87	-	100
Feb 88	20	80
Mar 88	7.32	92.68
Apr 88	-	100
May 88	-	100
Jun 88	-	100
Jul 88	5.26	94.74
Oct 88	12.50	87.50
m.N 88	19.44	80.56
f.N. 88	15.79	84.21
Dec 88	6.25	93.75

The lack of correspondence between inseminations and the degree of ovariole maturity seems to indicate that copulation occurs independently of the physiological state of the ovary. On the other hand, in other *Onitini* such as *Onitis caffer*, an empty spermatheca is generally associated with an undifferentiated ovary and a full spermatheca with a differentiated ovary (Edwards, 1986). In studies on *Phanaeus, Canthon, Liatongus,* and *Eurysternus,* Halffter & Martínez (1980) and Halffter & López (1980) found that copulation occurs when the first oocyte(s) approach maturity. In these cases copulation determines full maturity which is not achieved if copulation does not take place. A similar situation is seen in *Geotrupes cavicollis* Bates, where complete maturity of the oocytes, one for each ovary, marks the onset of nesting, with the female digging a gallery and the male joining her for copulation (Halffter, López & Halffter, 1985).

Analysis of fat-body accumulation.

In many *Scarabaeidae,* there is a relatively long lapse between the emergence of the adult and the first nesting. During this period the female feeds intensely and the develops gonad. As pointed out by Huerta, Anduaga & Halffter (1981), the existence of this period of maturation feeding is due to the fact that most adults emerge with scanty metabolic reserves. To check the existence of this period in the species studied, we examined the fat-body accumulated in the abdomen of each beetle (Table 8). It was seen that during the initial stages, the individuals still conserve fat-body from the larval and pupal stages (fat-body values were above grade 2) and that parallel to the progressive development of the ovary (Fig. 8) the individuals initiate an active feeding period as reflected in the progressive increase in fat reserves (Fig. 9).

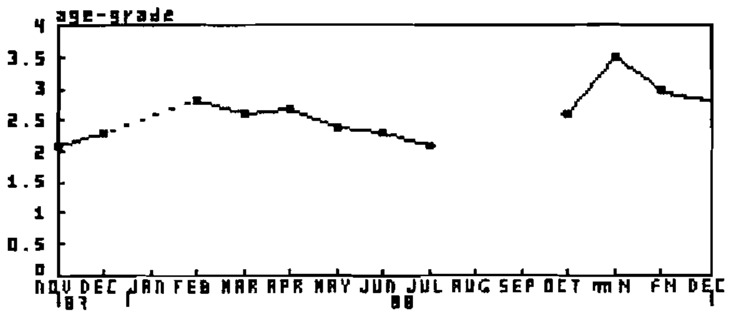

Fig.9. Evolution of the monthly average of fat-body accumulation in the abdomen of *Bubas bubalus* females, taking into consideration 5 categories (from 0 to 4) of lesser to greater abundance. Due to the difficulty of catching individuals during January, the discontinuous line represents the assumed evolution. m.N. = mid-November; f.N. = end of November.

The amount of fat reserves decrease once the first laying period starts (confirmed by the presence of yellow body from April, m.s. in preparation). The amount of fat reserves decrease. The further advanced the nesting period, the more this become apparent, suggesting that feeding is scarce during this period.

At the end of November and in December 1988 there was an important decline in fat-body reserves. This may be explained by the less favourable environmental conditions during this year as compared to 1987. Thus, as with other dung beetles such as *Oniticellus intermedius* (Reiche) (Tyndale-Biscoe, 1978), *Bubas bubalus* females mobilise the fat reserves stored in the abdomen, and thus reduce them, in response to situations of stress.

Bubas bubalus* nests

The nests found, of the paracoprid type (Bornemissza, 1976), are listed in

*The difficulty involved in following nesting of the species in the field, as is the case in this study, causes our observations to be a contribution to studies made on *Bubas bubalus* by other authors (Klemperer,1981) under laboratory conditions where nesting habits can be followed exactly.

Table 8

Number of *Bubas bulabus* females in each category of fat-body established.
m.N = mid-November; f.N = end of November.

Month of examined	Categorie of fat-body				
	0	1	2	3	4
Nov 87	-	11	29	14	1
Dec 87	-	5	2	5	1
Feb 88	-	-	5	8	2
Mar 88	-	2	16	15	10
Apr 88	-	6	5	13	10
May 88	-	2	5	9	5
Jun 88	-	7	-	3	7
Jul 88	-	3	6	7	2
Oct 88	-	2	8	5	3
m.N 88	-	2	6	13	17
f.N 88	-	1	5	6	8
Dec 88	-	3	4	6	5

Table 9. It should be pointed that we used cattle faeces, with a low water content (deposited more than a week before) and with an average of minimum and maximum diameter of 28.41 and 31.29 cm. No relationship was found between the number of surface hole and the number of individuals under the dung. In some cases, a high number of holes was associated with a small number of beetles, whereas in others the situation was the opposite. This suggests that the individuals first enter one dung pile to feed and then leave it to go to another. This behaviour is repeated continually until nesting. It should be remembered that we recorded flight activity for both males and females during the nesting period. Such activity disappears completely in August and September, corresponding to the period of larval development. Larva in different stages of development were found only in these two months.

Nesting is sometimes not completed because of diverse external factors (dry, hard soil; unsuitable dung, etc.). This might be why we found nests containing dung but not adults, eggs, or larvae. In one case observed on 16-VII-86 the buried dung belonged to a feeding chamber near the nesting area, as occurs with various species of the tribe *Coprini* (Huerta, Anduaga & Halffter, 1981).The holes lead to vertical nesting chambers situated at a depth varying from 8 to 35 cm.

Table 9

Nests of *Bubas bulabus* examined during 1986 and 1987. The data in brackets correspond to the same faeces. f = adult females; m = adult males.

Date of observation	Minimum & maximum diameteter (cm) of the pad	Nests characteristics			
		depth (cm)	no.of eggs	no. of larvae	"sausage"
2-VII-86	33 & 33	9	4	-	not adults
		16	2	-	not adults
16-VII-86	33 & 33	10	1	1	not adults
		10	-	-	not adults
30-VII-86	32 & 38	15	-	-	not adults
		10	-	-	not adults
	33 & 33	13	-	-	not adults
		21	-	4	not adults
		8	-	1	not adults
	20 & 20	8	-	1	not adults
		22	-	9	not adults
	22 & 23	8	-	1	not adults
		22	-	9	not adults
13-VII-86	32 & 37	22	-	3	not adults
	22 & 24	20	-	4	not adults
	27 & 30	14	-	-	not adults
	29 & 38	22	-	4	not adults
	32 & 37	30	-	6	not adults
27-VIII-86	27 & 30	15	-	1	not adults
10-IX-86	30 & 32	-	-	1	not adults
	26 & 27	-	-	3	not adults
11-IV-87		35	1	-	not adults
	23 & 28				80 gr. 50 ml
		35	1	-	not adults
					55 gr. 25 ml
		17	-	-	2 f. & 1 m.
	28 & 35				60 gr. 30 ml
		17	-	-	1 f. & 1 m.
					65 gr. 35 ml
	33 & 34	15	1	-	1 f. & 1 m.

In April eggs were found, with and without adults, at the end of long brood masses (sausage-shaped), with an average weight and volume of 65 g. and 35 ml. respectively. These data agree with those indicated by Klemperer (1981). However, this author states that the presence of two eggs in each mass, one at each end, is a characteristic which defines the genus *Bubas* and separates it from other *Onitini*. In general, our observations confirm the existence of only one egg; four were found in only one case and two in another.

To conclude, the life cycle of *Bubas bubalus is* completed in one year in our study area and not in two as suggested by Klemperer (1981), who explains it in terms of a delayed metamorphosis. In our study females with pronounced tibial wear were never observed during the October-November period (Table 4), which indicates that individuals from the previous generation did not exist.

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