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Life cycle of the dung beetle *Onthophagus cervus* (Fabricius, 1798) (Coleoptera: Scarabaeidae: Scarabaeinae) in moist belts of south India

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ABSTRACT: Biology, nesting behaviour, and the factors favouring the high abundance of prominent dung beetle species, *Onthophagus cervus* (Fabricius, 1798) in an open agricultural field in North Kerala were studied. Short life cycle with high fecundity, low egg mortality, shorter larval duration, shorter developmental period, short generation time, female-biased sex ratio, and longer survivability of females were recorded. Female-biased sex ratio in *O. cervus* indicates that mating competition takes place between male offsprings and the high cost of producing males led to their reduction. Broad categorization of *Onthophagus* species is provided based on the comparison of data of brood mass production, fecundity, duration of egg, larval, pupal, adult stages, adult mortality and life span of various *Onthophagus* species. Higher abundance of *O. cervus* in the region is attributed to traits that are characterize of ***r***-selection such as high fecundity, small body size, low egg mortality, shorter larval duration, early onset of maturity, and shorter developmental period. Short generation time which enables attaining maturity earlier together with female biased sex ratio, longer duration of females favouring high egg production and shallow tunnels which enable easy and fast tunnelling process and development in thin soil top soil layer are the other factors that contributed to the higher abundance of *O. cervus*. Present study showed that geographic region wise knowledge on the life history traits of prominent dung beetles are necessary for interpretation of the exact mechanism behind their seasonality and abundance in specific regions and the generated data will be useful for the conservation of species in natural habitats.

KEY WORDS: Onthophagini, fecundity, sex ratio, male and female longevity, nesting behaviour

INTRODUCTION

Scarabaeid dung beetles (Scarabaeidae) belong to three distinct taxonomic groups, Scarabaeinae, Geotrupinae, and Aphodiinae (Baraud, 1985). Within the sub families, Scarabaeinae is the only group that is predominantly coprophagous. They feed on decomposing matter, carrion, decaying fruits, and fungi (Hanski and Cambefort, 1991). Dung beetles are one of the most important invertebrate contributors to dung decomposition in both temperate and tropical agricultural grasslands (Gittings *et al.,* 1994; Davis, 1996a,b; Horgan, 2001; Lee and Wall, 2006; Slade *et al.,* 2011; Kaartinen *et al*., 2013). Dung removal (Slade *et al.,* 2011), nutrient cycling (Menendez *et al.,* 2016; Nervo *et al*., 2017) seed dispersal (Lugon *et al*., 2017), and reduction of greenhouse gas emissions (Piccini *et al*., 2017) are the major ecosystem services provided by dung beetles.

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Analysis of the structure and local distribution of dung beetle assemblages in different biogeographic regions showed that dominant dung beetle species varies among different regions (Nealis, 1977; Doube, 1983; Janzen, 1983; Davis, 1993; Davis, 1998; Davis and Sutton, 1998; Davis *et al*., 2002). *Canthon histrio* Serville, 1828, *Onthophagus hirculus* Billberg, 1815, and *Deltochilum verruciferum* Felshe, 1911 are prominent species in Brazilian dry forest (Novais *et al*., 2016); *Dichotomius amplicollis* Harold, 1869, *Deltochilum gibbosum* (Fabricius, 1775) and *Onthophagus landolti* Harold, 1880 in Mexican dry forest (Andresen 2005, 2008); *O. wallacei* Harold, 1871, *O. fuscostriatus* Boucomont, 1914 in Indonesian forest (Shahabuddin, 2010); *O. vulpus* Harold, 1877, *Sisyphus thoracicus* Sharp, 1875 in a tropical rainforest in Malaysia (Davis, 2000); *Oniticellus pseudoplanatus* Balthasar, 1964 in moist forests of Ivory Coast (Cambefort and Walter, 1991); *Caccobius vulcanus* (Fabricius, 1801), *O. centricornis* Fabricius, 1798, *Tiniocellus spinipes* Roth, 1851, *Caccobius ultor* Sharp, 1875, *O. cervus* (Fabricius, 1798) and *O. dama* (Fabricius, 1798) in the moist belts of south India (Vinod, 2009; Sabu, 2011; Sabu *et al.*, 2011; Simi *et al*., 2012); *Digitonthophagus gazella* (Fabricius, 1787), *O. rectecornutus* Lansberge, 1883, *Copris repertus* Walker, 1858, *C. fricator* (Fabricius, 1787) in Deccan region in south India (Veenakumari and Veeresh, 1994, 1996); *Catharsius pithecius* (Fabricius, 1775) and *Gymnopleurus cyaneus* (Fabricius, 1798) in the agriculture belts in Maharashtra (Patole, 2019) and *Tiniocellus spinipes* Roth, 1851, *Tibiodrepanus sinicus* Harold, 1868, and *Caccobius ultor* Sharp, 1875 in the forests of Haryana in North Western India (Mittal, 2005; Kakkar and Gupta, 2009, Kakkar 2010). However, lack of knowledge on the biology and ecology of prominent dung beetles makes interpretation of the exact mechanism behind their seasonality, abundance and conservation strategies to be adopted in the natual habitats in specific regions impossible (Vinod 2009; Latha, 2011; Nithya, 2012; Sabu, 2012; Sobhana, 2014; Subha, 2017). A quick review revealed that except for the data available on the reproductive biology of *O. hirculus* in Brazil (Gonzalez and Morelli, 1999), *O. landolti* in Mexico (Pérez-Cogollo *et al*., 2015), *O. rectecornutus* Lansberg 1883, *Copris repertus* Walker 1858 and *C. fricator* Fabricius 1787 in south India (Veenakumari and Veeresh, 1994, 1996), reproductive biology of other prominent dung beetles is not available. The present study has been undertaken to understand the life history traits of the prominent dung beetle species, *O. cervus* in the moist belts of south India.

MATERIAL AND METHODS

Adult *O. cervus* beetles were collected using dung baited pitfall traps and hand picking from an open agricultural field at Naduvattam, Malappuram district, Kerala (India) (10^{0}52’55.92"N, 76^{0}0’29.59"E) during June 2016 to December 2017 period. Pitfall traps made of plastic basins, 10 cm in diameter and 15 cm deep with the minimum quantity of water to prevent the drowning of the fallen beetles, were placed in the field during 8:00 am to 12:00 pm. Preliminary verification and separation and sexing of the collected beetles were done by comparing with verified specimens and based on the morphological characters and taxonomic keys in Arrow (1931). Based on morphological characters such as small body size and colour, beetles of uniform age were selected and grouped. Ten mating pairs were selected, each pair was placed in an individual wide mouthed earthen pot with (diameter 51.5 cm, thickness 0.9 cm, and length 14 cm) and filled with finely sieved clay soil collected from the collection site and moistened with water with a depth of 13.5 cm and fresh cow dung on top for food and the construction of brood balls and each pair were provided with fresh cow dung twice a week. Top of the earthen pots was covered with mesh net (mesh size 0.053 µm) to prevent the escape of the beetles and the pots were kept at controlled room conditions (Temperature 23^{0}C-25^{0}C; humidity 75%). Water was sprayed with a mist sprayer on alternate days to prevent desiccation. Daily observations for all life events, such as brood ball formation, egg-laying, egg hatching, duration of the larval and pupal phase, and adult emergence were noted and parallel laboratory culture was maintained for observing each life cycle stage of the development and also for studying the nest architecture. In order to monitor the life cycle and development of egg, different stages of larval development, pupa and until adult emergence were recorded by making a small opening on each brood ball, which was closed by pasting with a layer of dung and soil after each observation and the brood masses/balls were retained in individual earthen pots arranged with moist soil. Observations were made twice a week until the emergence of new adults. Number, length and width of the brood masses, number of larvae, pupae and adults, and the size of the adults were recorded. Newly emerged beetles were collected, paired and counted and transferred to new individual earthen pot topped with fresh cow dung and were kept until their natural death. Adult longevity (after emergence from their brood ball) is known only in laboratory reared specimens and the survival period was noted for each individual beetle. Experiment set up was kept moist by sprinkling water to prevent desiccation.

Preliminary analysis was done in the field beneath the dung pats to get an idea about the tunnelling behaviour; brood ball construction, nesting preparation, and also open the tunnels by digging in the agriculture field from where the beetle collections were made. For the study of the nest architecture, adult beetles got from the collection site, were placed in plastic pots (15×15×16 cm) which was cut into half lengthwise and re-joined with masking tape to retain their original shape. The re-joined plastic pot was filled with moist soil up to a depth of 12 cm and topped with fresh cow dung droppings. Beetles were transferred to the pre-arranged plastic pot containing soil and cow dung topping. Top of the plastic pot was covered with a mesh net, after introducing the beetles to prevent their escape. The experiment setup was kept moistened by sprinkling water to prevent desiccation. After two weeks, the plastic pot was opened into two halves vertically with care, and the notes were being made on the nest architecture and the length of the tunnel was taken. Photographs were taken using Nikon digital camera D90 and Leica S8APO (Trinocular stereo zoom microscope).

RESULTS

Biology of *Onthophagus cervus*: The life biology involved four stages namely egg, larva, pupa, and adult. Egg stage lasted for 3.60±0.51 days, the larval stage for 16.70 ±1.87 days, the pupal stage for 10.20±1.03 days, and adult stage for 60.17± 2.08 days.

Brood mass and eggs (Fig. 1A-N): Adult beetles constructed brood balls after 12.4±0.69 days. A single mating pair produced 14.10±5.69 brood balls during its period of the life cycle. Oval shaped brood balls have a length of 20.4±0.97 mm, width 32.8±1.62 mm and were coated by a layer of soil and dung (Fig: 1A). The brood masses were formed of dung mass with an egg chamber with the egg glued to the wall of the egg chamber (Fig. 1B). Brood masses were attached to the wall and end of the tunnels. Eggs were elongate oval in appearance and creamy white, during the first two days. Prior to hatching (3^{rd} day), egg became yellowish and the egg shell became transparent (3^{rd} and 4^{th} day) and the larva was clearly visible through the chorion. Egg stage lasted for 3.6±0.51 days. A single mating pair produced 21.7±6.69 surviving eggs during its life time. Low egg mortality (14.57%) was recorded.

Larva: Three larval instars (Fig. 1C, D, E) were recorded. Newly emerged larvae were transparent with the tips of the mandible being dark brown. Larvae were found in a cavity inside a brood ball and they consumed the dung ball from inside. Newly hatched larvae were creamy white fleshy “grubs”. All larvae have the characteristic “coprine hump” and the flattened, fleshy-lobed anal segment. The larval period lasted for 16.7±1.87 days. Low larval mortality (16.12%) was recorded. A single mating pair produced 18.2±6.58 surviving larvae.

Pupa: Pupae were present inside the thin walled pupal cell or cocoon constructed by larva inside the brood ball. Inner surface of the pupal cell was smooth and were coated with soft dried dung and soil (Fig. 1F). Newly formed pupae were creamy white, shiny, with four pairs of finger-like processes on the dorso-lateral region of the abdomen and a large, blunt pronotal projection extending over a posterior portion of the head. Later on, the pupae turned golden brown in colour (Fig. 1G, H). The pupal period lasted for 10.2 ± 1.03 days. Pupal mortality (27.48%) was recorded. A single mating pair produced 13.2±4.88 pupae.

Adult: Teneral period lasted 2.40 ±0.51 days. The teneral adult was light orange-red in colour (Fig: 1, I). Adult emerged by cutting a hole in the brood ball (Fig. 1J). 67.42% of adults emerged (30 females and 10 males) and the sex ratio of 3:1 was observed. Newly formed adults took 1.40±0.52 days for the complete melanisation. On exit from the brood ball, newly emerged beetles constructed the tunnels. Sexual maturity was attained by 11±1.05 days of emergence. Adult male (Fig. 1K) duration of 35.2±8.65 days and female (Fig. 1L) duration of 60.17± 2.08 days were observed. Egg to teneral adults, took 28.2 ±1.03 days. A single mating pair produced 4±2.21 surviving adults during its life time.

Nesting behaviour: Adult beetles (males and females), upon releasing, made vertical (Fig. 1M) and horizontal tunnels (Fig. 1N). Both males and females were involved in tunnel construction and handling of dung. Both vertical and horizontal tunnels were made and were interconnected. Vertical tunnels with a depth of 6.96±1.30 cm and horizontal tunnels were with a length of 2.25±0.59 cm, were observed. Brood masses were present at the bottom of the tunnels. Brood balls were seen in single or in mass.

DISCUSSION

The present study provides data on the reproductive biology and life span of *Onthophagus cervus* and also enabled comparison of data with other *Onthophagus* species. Comparison of data on brood mass production, fecundity, duration of egg, larval, pupal, adult stages, adult mortality and life span of *O. cervus* with other *Onthophagus* species revealed that a broad categorization of *Onthophagus* species based on the life cycle characteristics are possible. Data on the brood mass production of different *Onthophagus s*pecies showed that *Onthophagus* species can be categorized as high and low brood mass producers. *Onthophagus stylocerus* (Samper and Piera, 1995); *O. rectecornutus* (Veenakumari and Veeresh, 1996); *O. lentolti* (Pérez-Cogollo *et al.,* 2015); *O. catta* (Gaikwad and Bhawane, 2016), and *O. cervus* comes under the category of high brood mass producers with a brood mass range of 1–40 and *O. hirculus* (Gonzalez and Morelli, 1999); *O. incensus* (Huerta and Garcia, 2013); *O. lecontei* (Arellano *et al.,* 2017) falls under the category of low brood mass producers with a brood mass range of 1–10. Similarly based on the size of brood ball two categories of *Onthophagus* species are recognizable with a large sized brood ball category consisting of, *O. stylocerus* (Samper and Piera, 1995); *O. rectecornutus* (Veenkumari and Veeresh, 1996); *O. catta* (Gaikwad ánd Bhawane, 2016) and small brood ball category of *O. medorensis* (Hunter *et al.,* 1991); *O. depressus* (Hunter *et al.,* 1996); *O. hirculus* (Gonzalez and Morelli, 1999); *O. lecontei* (Arellano *et al.,* 2017), and *O. cervus.*

Duration of egg incubation revealed a pattern of longer egg incubation period in *O. medorensis* (Hunter III *et al*., 1991.); *O. stylocerus* (Samper and Piera,1995); *O. depressus* (Hunter *et al.,* 1996); *O. rectecornutus* (Veenakumari and Veeresh, 1996); *O. hirculus* (González-Vainer and Morelli, 1999); *O. incensus* (Huerta *et al.,* 2010), *O. cervus,* and short egg incubation period in *O. landolti* (Pérez-Cogollo *et al*., 2015); *O. catta* (Gaikwad and Bhawane, 2016), and in *O. lecontei* (Arellano *et al.,* 2017).

Comparison of larval duration showed that *O. cervus* and *O. rectecornutus* (Veenakumari and Veeresh, 1996) belong to the shorter larval duration category compared to *O. medorensis* (Hunter *et al.,*1991*); O. stylocerus* (Samper and Piera, 1995); *O. depressus* (Hunter *et al.,*1996); *O. incensus* (Huerta *et al.,* 2010); *O. landolti* (Pérez-Cogollo *et al*., 2015); *O. catta* (Gaikwad and Bhawane, 2016)*;* and *O. lecontei* (Arellano *et al.,* 2017) with long larval duration period. Comparison of pupal duration among the various *Onthophagus* species show that *O. landolti* (Pérez-Cogollo *et al*., 2015) has short pupal period compared to longer pupal duration in *O. medorensis* (Hunter *et al.,* 1991); *O. stylocerus* (Samper and

Fig. 1A) Brood ball of *Onthophgus cervus,* B) Egg glued to the wall of brood mass, C) First instar larva, D) Second instar larva, E) Third instar larva, F) Pupal cell, G) Pupa - early phase, H) Pupa - late phase, I) Teneral adult, J) Emergence of adult from pupal cell, K) Adult male, L) Adult Female, M& N) Nesting behaviour - vertical & horizontal tunnels.

Piera, 1995); *O. depressus* (Hunter *et al.,* 1996); *O. rectecornutus* (Veenakumari and Veeresh, 1996); *O. catta* (Gaikwad and Bhawane, 2016); *O. cervus,* and *O. lecontei* (Arellano *et al.,* 2017). Higher variability in egg hatchability, larval and pupal survivability under uniform conditions in many samples indicate that wider variation exists in the population and the exact reasons are not understood and could be genetical.

Developmental period of *O. cervus* (egg to a teneral adult) and Mexican species *O. landolti* (Pérez-

Table 1. Fecundity, egg mortality, egg hatchability, larval survivability, pupal survivability and adult mortality of *Onthophagus cervus* in the moist belts of south India

Parameters	Mean ±SD	(%)
Fecundity (No of eggs per female)	25.4±6.67	-
Egg hatchability	21.7±6.69	85.43
Egg mortality	3.7±2.31	14.57
Larval survivability	18.2±6.58	83.88
Larval mortality	3.5±1.50	16.12
Pupal survivability	13.2±4.88	72.52
Pupal mortality	5±2.62	27.48
Adult survivability	4±2.21	30.30
Adult mortality	9.2±2.57	69.69

Cogollo *et al.,* 2015) was the shortest among the various *Onthophagus* species. Teneral adult period was shorter in *O. cervus* compared to other *Onthophagus* species. Comparison of adult duration showed that *O. cervus* and *O. medorensis* (Hunter *et al.,* 1991); *O. depressus* (Hunter *et al.,* 1996); *O. landolti* (Pérez-Cogollo *et al*., 2015); *O. lecontei* (Arellano *et al.,* 2017); were species with short adult longevity whereas, *O. stylocerus* (Samper and Piera, 1995); *O. rectecornutus* (Veenakumari and Veeresh, 1996); *O. incensus* (Huerta *et al.,* 2010); and *O. catta* (Gaikwad and Bhawane, 2016); were with longer adult duration. Low pupal survivability compared to the high egg hatchability, larval survivability, and adult survivability of *O. cervus* indicated that the pupal phase as the crucial phase in the life cycle of *O. cervus*.

Type 1 pattern of nesting was present in *Onthophagus cervus* with simple, shallow tunnel with bottom containing brood masses and with vertical and horizontal tunnels (Halffter and Edmonds, 1982). Similar type 1 pattern was reported in *O. taurus* (Fabre, 1918); *O. fucatus* (Main, 1922); *O. coenobita* (Burmeister, 1930); *O. catta* (Gaikwad and Bhawane, 2016); and *O. lecontei* (Arellano *et al.,* 2017). Some *Onthophagus* species constructed compound nest (Type 2) with galleries that may have one or more branches, which ended in to brood cells in *O. nuchicornis* and *O. fracticornis* (Burmeister, 1930); *O. medorensis* (Hunter *et al.,* 1991); *O. stylocerus* (Samper and Piera, 1995); *O. rectecornutus* (Veenakumari and Veeresh, 1996); and *O. incensus* (Huerta and Garcia, 2010) .

Among the tunneling species, large species tend to bury their brood balls at a deeper depth and small species at shallower depth which helps to reduce overall competition for nesting space (Hanski, 1991a; Rougon and Rougon, 1991; Hernández *et al.,* 2011).Tunnels were dug roughly perpendicular to the interface between soil and dung, resulting in interference competition for nesting space underneath dung pads, especially in areas where tunnels branch out into nesting chambers (Halffter and Edmonds, 1982; Hanski, 1991b; Anna *et al.,* 2016). Higher longevity of females and sex ratio biased towards females were seen in *O. cervus.* Why females live longer than males are generally unknown, either metabolic differences or differences in patterns of resource allocation between males and females probably account for the gender difference in lifespan (Fox *et al*., 2003). Alternatively, males may allocate a greater proportion of their biomass to the reproduction, or allocate those resources sooner, such that they become resource-stressed at a younger age. Gender-difference in energy expenditure explains at least some of the gender-difference in lifespan. Some of the difference in lifespan and mortality rates between genders is due to faster energy-water loss in males than in females (Fox *et al*., 2003).

Observed sex ratio bias in *O. taurus* females, is caused by the higher mortality of male and suggested that this might be linked to higher demand for nutritional resource during the development of offspring (Clarissa *et al.,* 2010). Differential mortality is common in species like dung beetles with both the sexes having distinct nutritional requirements and energy expenditures as a result of differential mobility and investment in parental care (Veran and Beissinger, 2009). Evaluation of the cost of male production studies with other groups (Jokela *et al*., 1997; Wolinska and Lively, 2008; Anna *et al.,* 2019), have suggested that there is a cost of producing males. Also, as per LMC (local

Table 2. Number and size of brood balls and duration (days) of different life stages of different *Onthophagus* species

Species	Brood ball			Duration (days) of different life stages					
	No.	Length (mm)	Width (mm)	Egg	Larva	Pupa	Teneral adult	Total	Adult longevity
O. cervus (present study)	14.1± 5.69	20.4± 0.97	32.8± 1.62	3.6± 0.51	16.7± 1.87	10.2± 1.03	2.4± 0.51	28.2± 1.03	60.17± 2.08
O. catta (Gaikwad and Bhawane, 2016)	22.5 ± 17.67	27.7± 3.79	5.4 ± 1.49	2.38 ± 0.8	31.5 ± 6.37	13.46 ± 0.8	3.5 ± 0.70	48.33 ± 4.49	66.7± 11.98
O. depressus (Hunter *et al*., 1996)	ND	22 ± 4.24	16 ± 1.41	3.4 ± 1.28	27	12	3	46.5 ± 14.84	50
O. incensus (Huerta *et al*., 2010)	5 ± 5.65	25 ± 7.07	12.5 ± 3.53	4	22	10 ± 2.82	ND	36 ± 2.82	93
O. *landolti* (Perez cogollo *et al.*, 2015)	14.5 ± 13.43	ND	ND	2.2± 0.70	21± 1.41	7 ± 1.41	ND	30	60
O. lecontei (Arellano *et al*., 2017)	3.50 ± 1.74	23.47± 1.52	23.14 ± 0.91	2	22± 1.14	11± 0.87	4± 0.95	39	60 ± 2.3
O. medorensis (Hunter *et al*., 1991)	ND	10.27± 4.63	ND	4	28	11.5 ± 0.70	4± 1.41	49.5 ± 4.94	53 ± 26.88
O. stylocerus (Samper and Piera, 1995)	19.75 ± 2.16	31.5 ± 9.19	15.5 ± 3.53	7.5 ± 3.53	22.33 ± 3.05	14 ± 4.24	15	60.5 ± 13.43	ND

Author details are provided in parenthesis; ND: no data available

mate competition), female-biased sex ratio is favored if mating competition takes place between male offspring (Hamilton, 1967), whereas an equal sex ratio is expected under random mating (Fisher, 1930). Hence the female-biased sex ratio noticed in *O. cervus* indicate that mating competition takes place between male offspring and the high cost of producing males might have led to the reduction in the ratio of males to females in *O. cervus.*

Traits that are common in an ***r***-selected species such as high fecundity, small body size, low egg mortality, shorter larval duration, early maturity onset, and shorter developmental period (short generation time enables attaining maturity earlier together with female biased sex ratio), longer duration of females (favouring high egg production) and shallow tunnels (which enable easy and fast tunnelling process and development in thin soil top soil layer) contribute to the higher abundance of *O. cervus* and makes it a prominent dung beetle species in the moist belts of south India.

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