ORIGINAL PAPER

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Patterns of daily flight activity in onitine dung beetles (Scarabaeinae: Onitini)

Abstract Different species of African dung beetles emerge from the soil at characteristic times of the day to fly and colonize the freshly-deposited dung of mammalian herbivores. Onitine dung beetles in their natural habitat displayed one of five distinctive daily flight behaviours: dusk crepuscular (*Onitis alexis* Klug, *O. caffer* Boheman, *O. fulgidus* Klug, *O. tortuosus* Houston, *O. vanderkelleni* Lansberge, *O. westermanni* Lansberge); dusk/dawn crepuscular (*O. pecuarius* Lansberge and *O. viridulus* Boheman); dusk/dawn crepuscular and nocturnal (*O. aygulus* (Fabricius), *O. mendax* Gillet, *O. uncinatus* Klug); late afternoon-dusk and dawn-early morning [*Heteronitis castelnaui* (Harold)]; or diurnal flight activity [*O. belial* (Fabricius), *O. ion* (Olivier)]. These diagnostic daily flight behaviours span a light intensity range of over 6 orders of magnitude and have been retained in selected species introduced into Australia. Ambient light intensity appears to be the primary determinant of the daily flight period in onitine dung beetles. Because the dung of mobile herbivores is rapidly exploited by onitine species for feeding and breeding purposes, different flight behaviours result in a spatial and temporal partitioning of species in the local dung beetle community. The timing of flight may contribute to, or lead to avoidance of, competition between species which may ultimately affect colonization success. Many onitines show a strong preference for dung of specific herbivores, which may further reduce interspecific competition. All crepuscular-nocturnal species examined raised their thoracic temperatures endothermically to between 35 °C and 40 °C before the onset of flight. In *O. aygulus* the thoracic temperature excess was as large as 19.3 °C. The thermal threshold below which the frequency of flight onsets drops off rapidly is about 12 °C for *O. aygulus* and 17 °C for *O. alexis* and *O. pecuarius*. Radiant loss of body heat during cool nights and dawns may explain why smaller species (< 0.4 g body weight), in particular, are adapted behaviourally so that they fly only during the day or early dusk.

Key words Flight behaviour · Diel activity · Dung beetles · Endothermy

Introduction

During the wet season in the savannah of sub-Saharan Africa, various species of dung beetle may be seen flying at different times of the day in search of fresh herbivore dung, in which they feed and mate (Gill 1991; Hanski and Cambefort 1991). Daily flight activity in dung beetles may be broadly classified as diurnal, crepuscular or nocturnal, depending on the light levels at the time of day flight activity occurs. Behavioral diversity in daily flight times is presumably the consequence of intense interspecific competition among dung beetles for the dung of mammalian herbivores (Bartholomew and Heinrich 1978; Heinrich and Bartholomew 1979; Hanski and Cambefort 1991). Successful foraging in many dung scarabs requires several physiological adaptations not seen in most beetles, such as the maintenance of a constant elevated thoracic temperature while active (Bartholomew and Heinrich 1978; Heinrich and Bartholomew 1979) and a visual system that is able to operate in near-darkness (McIntyre and Caveney 1985). Endothermy has been

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shown to allow day-active scarabs to compete success-fully with others at the site of the dung resource (Bartholomew and Heinrich 1978). Night-active scarabs, too, raise and regulate their body temperature by endothermic means just before and during flight (Chown and Scholtz 1993), which presumably extends the seasonal and daily temperature range over which they are able to forage. By foraging on the wing in the dark, many dung scarabs are able to exploit herbivore dung voided at night before it becomes available to dawn- and day-flying species. Yet nocturnal scarabs must be able to see sufficiently well to avoid obstacles while flying rapidly over long distances in near-pitch darkness. In a dung beetle, the limit to perception is set by the maximum effective superposition aperture of its dark-adapted eye, which determines how much light falls onto the retina (Caveney and McIntyre 1981; McIntyre and Caveney 1985).

This paper describes the diel patterns of flight behaviour of 12 species of dung beetle belonging to a scarabaeine tribe, the Onitini, and correlates flight activity with associated ambient light and temperature conditions. A connection between flight behaviour, beetle size and thermoregulatory ability is suggested. The compound eyes in these onitine species are optically adapted to the light intensity at the time of peak flight activity (P. McIntyre and S. Caveney, unpublished work).

Materials and methods

Beetles

The genus *Onitis* comprises about 153 Afro-Indian species of medium to large beetles, while *Heteronitis* is an African genus of five large sub-Saharan species (Ferreira 1968–1969, 1978). Detailed observations were made on the flight behaviour of 11 species of *Onitis* [*O. alexis* Klug, *O. aygulus* (Fabricius), *O. caffer* Boheman, *O. fulgidus* Klug, *O. mendax* Gillet, *O. pecuarius* Lansberge, *O. tortuosus* Houston, *O. uncinatus* Klug, *O. vanderkelleni* Lansberge, *O. viridulus* Boheman, *O. westermanni* Lansberge) and *H. castelnaui* (Harold)] from large numbers of field-collected specimens or laboratory-reared specimens acclimated to natural light conditions. Small numbers of *O. belial* (Fabricius) and *O. ion* (Olivier) that were reared in the laboratory were also observed. Preliminary field observations were also made on small numbers of *O. deceptor* Peringuey and *O. picticollis* Boheman.

African material

Dung beetles were studied in midsummer in South Africa. Beetles were collected in their natural habitat near Skukuza (24.59S, 31.36E) in the Kruger National Park (*O. alexis, O. deceptor, O. fulgidus, O. mendax, O. picticollis, O. uncinatus* and *H. castelnaui*) or collected at cattle farms between Kaapmuiden (25.32S, 31.19E) and Komatipoort (25.26S, 31.56E) (*O. alexis, O. uncinatus* and *O. westermanni*). *O. aygulus* was collected near Grahamstown (33.19S, 26.33E) and Swellendam (34.05S, 20.26E) in the Cape Province and *O. caffer* at Parys (26.53S, 27.28E) in the Orange Free State.

Australian material

African dung beetles introduced into Australia were obtained either from colonies reared in the laboratories of the Division of Entomology of the Commonwealth Scientific and Industrial Research Organization (CSIRO) in Canberra, or collected at field sites in New South Wales (NSW) or Queensland (Qld) where they had been released as part of the CSIRO Dung Beetle Project and had become established (Waterhouse 1974). *O. alexis*, now widely established in eastern Australia, was collected mainly at Araluen (35.36S, 149.49E), southern NSW, but also at Grafton and Jackadgery (29.35S, 152.00E), northern NSW, and at Gayndah (25.35S, 151.39E), Qld. *O. aygulus* originated from a summer rain-fall strain from the northern and eastern Cape Province of South Africa and was collected in the field at Parkes (33.09S, 148.11E), NSW. *O. pecuarius* was field-collected at Moruya (35.56S, 150.06E), NSW, and at Toowoomba (27.32S, 151.56E), Qld; *O. viridulus* at Grafton and at Jackadgery, NSW; *O. tortuosus* at Tenterfield (29.00S, 152.00E), NSW; *O. caffer* at Moruya, and *O. vanderkelleni* at Mareeba (16.59S, 145.28E), Qld. *O. westermanni* was obtained from CSIRO stock in Canberra. The west Mediterranean species *O. belial* and *O. ion* were reared at CSIRO.

Field-collected beetles were identified with the help of Dr. Keith Houston with reference to the CSIRO collections in Canberra and Pretoria.

Flight trials

The method used to determine the flight time of each species was similar to that described in Houston and McIntyre (1985). Beetles were field-collected from beneath dung pads and observed in flight the same day or were kept well-fed for up to 4 days after collection in uncrowded conditions before observation. Synchrony and timing of flight often changed after longer periods in captivity. Laboratory-reared beetles were kept under natural light conditions for several days before testing. Beetles were sieved from the soil in holding bins containing ample fresh dung, counted and placed on lightly moistened screened loam in shallow basins (30 cm in diameter) several hours before the flight trial was due to start. Healthy beetles immediately burrowed into the soil; those that did not were replaced. Up to 200 beetles were placed in each basin. The basins were then placed in flight chambers at least 1 h before the expected time of flight onset.

Light and temperature

Light and temperature were recorded automatically by a data logger with two light channels and eight temperature channels at 2-, 5- or 10-min intervals. Light intensity was measured with a Photodyne radiometer Model 88XLC with Model 200 GaAsp sensor head, with flat sensitivity in the spectral range 400–800 nm (details in Houston and McIntyre 1985). The light intensities in Figs. 1–4 are the logarithms (to base 10) of the light readings in nW/cm^2. Soil and air temperatures in each flight chamber were measured with electronic thermometers. Thoracic temperatures of active beetles were measured with 40-gauge copper-constantan thermocouples, glued into hypodermic needles, and a Kane-May 457 XP digital thermometer (Chown and Scholtz 1993).

Results

Flight activity of Onitini

Flight activity data are plotted in Figs. 1–4, either as a function of time or of relative light intensity. Because

ambient light intensity is the dominant cue triggering flight under otherwise favourable environmental conditions (Houston and McIntyre 1985), flight activity is best plotted as a function of light intensity. This corrects for seasonal shifts in flight time and distinguishes between crepuscular and nocturnal flight patterns. Activity is crepuscular when numbers of active beetles increase as light intensity drops at dusk or climbs at dawn, whereas nocturnal activity is when numbers accumulate at near-constant low light intensities. Details of the flight experiments are given in Table 1. The 50% light level referred to in Table 1 and below is the light intensity at which 50% of the beetles that eventually flew had flown.

Crepuscular species

O. alexis The flight behaviour of this dung beetle, which has a very wide distribution in Africa (Ferreira 1978), was first described in Houston and McIntyre (1985). *O. alexis* flew at dusk only in our flight trials. In mid-summer onset of flight occurs a few minutes after sunset and flight ceases about 30 min thereafter. Although the chronometric time of flight shifts during the summer as sunset times change (Fig. 1a), flight occurs only during a narrow range of light intensity at dusk, both in the natural (South African) (Fig. 4) and adopted (Australian) habitat (Figs. 1b, 3b). Flight onset during dusk can be experimentally inhibited by shining day- or night-time levels of illumination onto the beetles (Houston and McIntyre 1985). This suggests that the normal flight window in crepuscular fliers is demarcated by absolute light intensity. *O. picticollis* is another *relatively* small species that, like *O. alexis*, has a flight restricted to early dusk.

O. pecuarius This crepuscular beetle has both a dusk (Fig. 2a) and a dawn (Fig. 2b) period of flight activity. At dusk, the pattern of flight resembles that of *O. alexis*. The numbers of flying beetles accumulate during dusk along a slightly shallower slope than those of *O. alexis* (Fig. 2c: compare with Fig. 1b). At dawn, the pattern of activity in *O. pecuarius* is the reverse of that seen at dusk (Fig. 2b), with mean flight onset occurring at a similar light intensity. However, flight onset at dawn occurs over a wider range of light intensities (Fig. 2d).

Because these two introduced species are abundant and widespread in Australia, they were routinely tested in flight trials alongside the species with more restricted distributions collected at the same locality. They provided a "reference flight pattern" in the experiments described below. This was convenient when beetles were removed from their field-collection sites and flight-tested in Canberra, because the mean flight onset time is also influenced by factors other than light intensity, such as temperature, starvation, local topography and wind. The timing of a reference flight of *O. alexis*
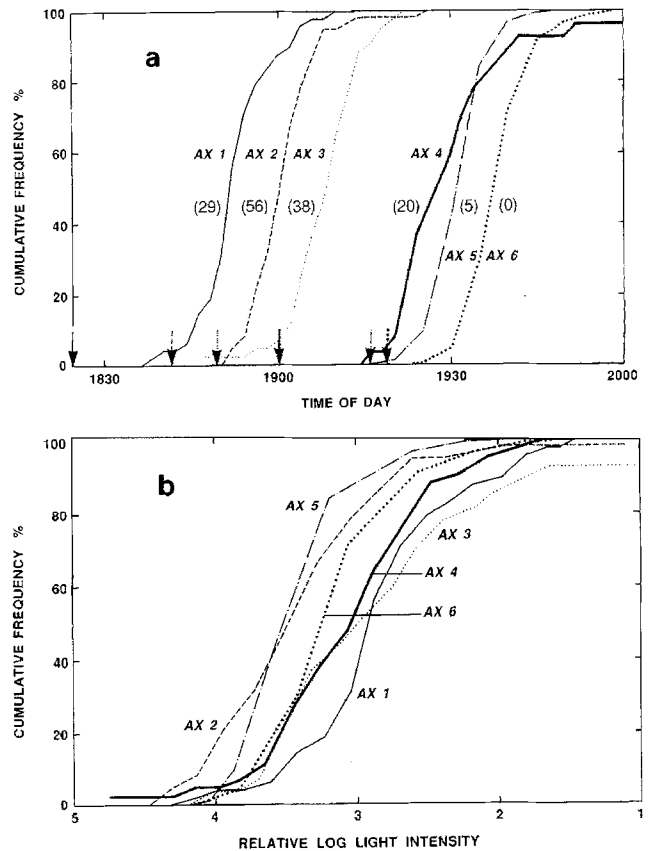

Fig. 1a, b Flight patterns in *Onitis*. Flight activity is displayed here as accumulated frequency of flight onsets as a function of time of day or of ambient light levels. Each *flight* curve has a *number code* referring to the experimental details listed in Table 1. Dusk flight activity of *O. alexis*. **a** The absolute time of flight changes during the summer, but remains approximately constant relative to sunset time (*arrows*) on the day of each flight trial. Each *curve* is ranked with a bracketed number referring to the day's position in relation to summer solstice (21 December: the *curve* on the *extreme right*). Over 90% of the beetles set flew within a 20-min period during dusk. **b** Flight activity as a function of light intensity during dusk. Flight takes place over a narrow range of light intensities. Same data as in **a**

was also useful in ranking the relative times of dusk flights of some species which may vary in different populations (for example *O. viridulus*). *O. tortuosus*.

Both laboratory-reared and field-collected beetles were flown in Australia, with similar results (Table 1). This species flew only during dusk. Although the duration of dusk flight in *O. tortuosus* is similar to that of *O. alexis*, mean onset of flight occurred about 0.4 log light intensity units earlier than that of the *O. alexis* reference flight. As this represents only 4 min of real time – the light intensity falls off rapidly at dusk – this may not be significant.

O. viridulus The flight pattern in this species resembles that of *O. pecuarius*, as it flies both at dusk and dawn. Dusk flight coincides with that of *O. alexis*, although the specimens collected at one site flew earlier at dusk.

Table 1 Details of flight experiments

Date Year/Day	Species	Code	Number set	Number flew	Light at 50%	Temp range	Locality collected	flown
85326	O. alexis	AX1	138	96	2.92	18–16	Grafton	Grafton
86046		AX2	166	131	3.28	28–26	Jackadgery	Moura
85028		AX3	42	42	3.05	23–22	Grafton	Grafton
86335		AX4	29	27	3.00	25–21	Parkes	Parkes
82350		AX5	224	219	3.50	22–21	Araluen	Canberra
82355		AX6	815	385	3.25	19–17	Araluen	Canberra
86344		AX7	30	28	3.35	27–26	Parkes	Canberra
85014		AX8	300	294	2.88	24–23	Araluen	Canberra
82104+		AX9	78	66	2.42	29–26	CSIRO	Canberra
87046+		AX10	164	132	3.20	32–32	Kaapmuiden	Kaapmuiden
91024+		AX11	60	47	3.30	32–27	Skukuza	Skukuza
85014	O. pecuarius	P1	300	282	2.95	24–23	Moruya	Canberra
85099		P2	71	48	3.00	19–18	Moruya	Moruya
85100		P3	69	60	2.90	21–19	Moruya	Canberra
85070		P4	163	155	2.82	21–19	Moruya	Canberra
85032		P5	296	85	2.50	17–17	Moruya	Moruya
85073		P6	60	58	3.07	23–22	Moruya	Canberra
85015*		P7	300	107	3.26	17–17	Moruya	Canberra
85033*		P8	254	63	3.13	17–17	Toowoomba	Toowoomba
86344	O. aygulus	AY1	225	164	0.5	27–17	Parkes	Canberra
86346		AY2	212	120	1.0	24–19	Parkes	Canberra
85326	O. viridulus	V1	220	80	3.63	18–16	Jackadgery	Grafton
85028		V2	257	219	3.10	23–22	Grafton	Grafton
85326		V3	220	45	2.94	18–16	Grafton	Grafton
85033*		V4	200	22	1.93	17–17	Grafton	Toowoomba
85030*		V5	364	85	2.20	20–19	Grafton	Grafton
85326*		V6	434	81	2.33	17–17	Grafton/ Jackadgery	Grafton
82104+	O. westermanni	W1	170	86	3.92	29–26	CSIRO	Canberra
87046+		W2	80	56	3.55	32–32	Kaapmuiden	Kaapmuiden
82350	O. tortuosus	T1	263	125	3.95	24–21	CSIRO	Canberra
86046		T2	175	135	3.72	27–26	Tenterfield	Moura
85099/100	O. caffer	C1	71	56	2.75	20–18	Moruya	Moruya/ Canberra
85070	O. vanderkelleni	K1	54	44	2.56	21–19	Mareeba	Canberra
85073		K2	51	36	2.27	23–22	Mareeba	Canberra
94006*	H. castelnaui	H1	≈50	39	1.85	18	Skukuza	Skukuza
94008*		H2	48	43	0.91	18	Skukuza	Skukuza
94009		H3	298	127	4.09	27–22	Skukuza	Skukuza
94010*		H4	171	76	3.21	20–21	Skukuza	Skukuza
94006	O. uncinatus	U1	≈300	216	1.06	23–19	Skukuza	Skukuza
94007		U2	≈300	201	1.05	23–20	Skukuza	Skukuza
94009		U3	125	77	0.69	23–22	Skukuza	Skukuza
94006	O. fulgidus	F1	70	22	2.46	23–22	Skukuza	Skukuza
94009		F2	159	32	1.74	23–22	Skukuza	Skukuza
94004	O. mendax	M1	≈130	110	1.3	24–23	Skukuza	Skukuza
94005		M2A	≈130	103	2.4	21–20	Skukuza	Skukuza
94005		M2B	≈100	40+43˙	1.9	21	Skukuza	Skukuza
94006*		M3	≈100	41	1.1	18	Skukuza	Skukuza
94007		M4	≈50	22	0.41	22–20	Skukuza	Skukuza
94010		M5	196	91	1.0	20–21	Skukuza	Skukuza

*Dawn flights. CSIRO = laboratory-reared beetles
+ Beetles flown under non-standard conditions. Flights W1 and AX9 are described in McIntyre and Caveney (1985). Flights W2 and AX10 were flown in South Africa under rainy conditions
˙The beetles in Flight M2A are the same as those in Flight M1, and the beetles in M2B the same as those in M3. The beetles of flight M2B were collected on the day of the flight. 40 of them flew during the dusk flight (1800–1940) and a further 43 had flown by 2130. These were all replaced for Flight M3
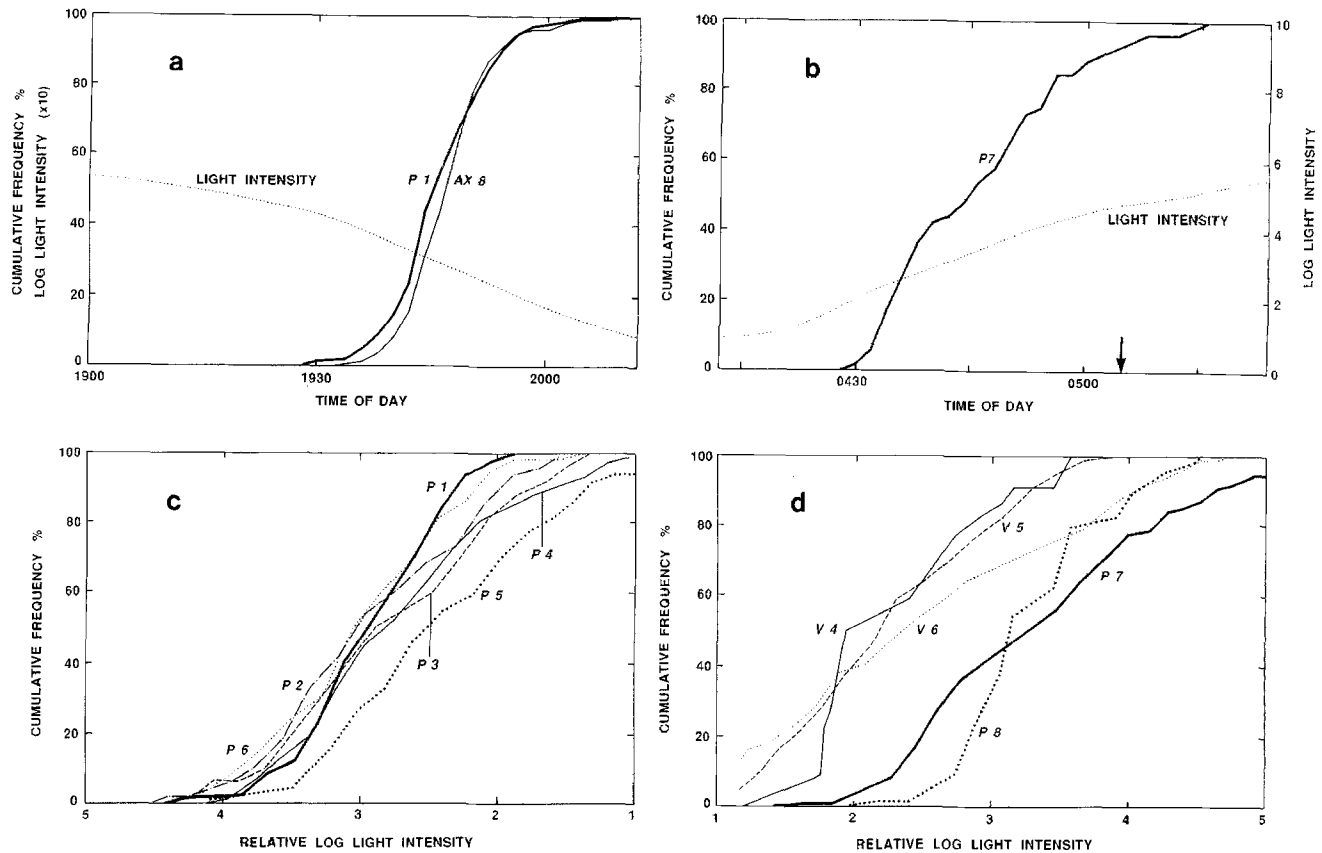
Fig. 2a–d Crepuscular flight activity in *O. pecuarius* and *O. viridulus*, plotted as in Fig. 1. Panels **a** and **b** are flight data obtained from the same beetles set up one afternoon, allowed to fly and then set up again before dawn the following morning and tested again; **c** and **d** amalgamate these data with those of several trials with other beetles. **a** Dusk flight activity of *O. pecuarius* is precisely timed and coincides with that of *O. alexis* tested concurrently. **b** Dawn flight extends over a longer time than that seen at dusk but main flight ceases before sunrise (*arrow*). *O. alexis* has no dawn flight. **c** Dusk flight activity as a function of light intensity in six separate trials. The slope of the flight curves of *O. pecuarius* is slightly shallower than that of *O. alexis*. Beetles start flying at a lower mean light intensity when soil temperature is low (*flight P5*). **d** Dawn flight activity as a function of light intensity in *O. pecuarius* and *O. viridulus*. The curves for *O. pecuarius* (*P7* and *P8*) are similar to those seen at dusk, suggesting that the shallower curve seen in **b** was due to a more gradual increase in light at dawn during this experiment. *O. viridulus* (*curves V4*, *V5* and *V6*) flies at relatively lower light intensities, both with respect to that of *O. pecuarius* and to its own dusk flight

The dawn flight of both populations of this species were synchronous. Dawn flight in *O. viridulus* is earlier than that of *O. pecuarius* (Fig. 2d).

O. westermanni and *O. fulgidus* These two species are exclusively early dusk fliers. *O westermanni* had a mean flight onset time marginally earlier than *O. alexis* in the two trials listed in Table 1. However, these *O. alexis* flights may be somewhat atypical (particularly flight AX9), because the trial was carried out under laboratory conditions. The flight period of *O. fulgidus* is iden-

tical to that of *O. alexis* (Fig. 4). These three species are commonly found together in cattle or buffalo dung pads.

Also listed in Table 1 are two other dusk-crepuscular species, *O. caffer*, which has a dusk flight pattern similar to *O. pecuarius*, and *O. vanderkelleni*, which has a relatively late and abrupt dusk flight.

Crepuscular/nocturnal species

O. aygulus The summer rainfall population of this species, collected in Australia, has an extended crepuscular/nocturnal flight pattern (Figs. 3a, b). Several of the beetles in the flight chamber flew soon after sunset, but the majority emerged from the soil at a fairly steady rate throughout the night to fly (Fig. 3a). The few beetles remaining in the soil flew at dawn.

O. mendax and *O. uncinatus.* The flight pattern of these two species is predominantly crepuscular although, when tested in the eastern Transvaal on the day of collection, both species contained individuals that flew off during the night (Fig. 4). On one occasion (of three-trials) many individuals of *O. uncinatus* flew during a moonless night.

Late afternoon/dusk–dawn/early morning species

H. castelnaui was exceptional among the onitine beetles examined in that its onset of flight occurred before
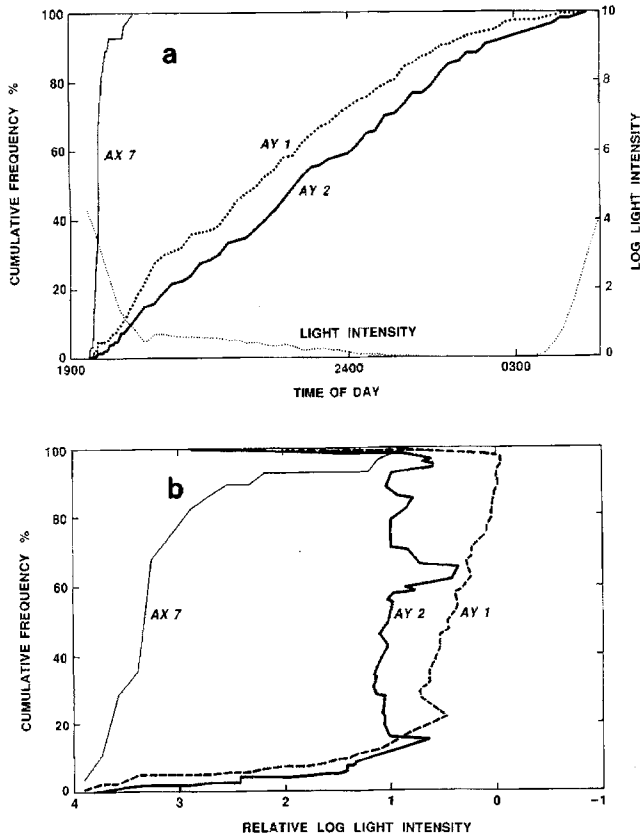
Fig. 3a, b Crepuscular-nocturnal flight activity in *O. aygulus*, plotted as in Fig. 1. **a** Results from two flights showing that although a few beetles fly at dusk and dawn, most fly at night. The flight pattern of *O. alexis* collected at the same site and flown in parallel is shown on the *left*. **b** Relationship between flight pattern in *O. aygulus* and light level, in comparison to that of *O. alexis*. The light intensity range at which 90% of *O. aygulus* flew was 2–3 log units lower than for *O. alexis*. Same data as in **a**

Fig. 4 Activity patterns of five sympatric onitine beetles flown on the same night in their natural habitat in the eastern Transvaal, plotted as in Fig. 1. Beetles were collected in the morning of the start of the flight trial from fresh elephant dung (*O. mendax* and *Heteronitis castelnaui*) or fresh buffalo dung (*O. alexis, O. fulgidus* and *O. uncinatus*). In the late afternoon 127 *H. castelnaui* (of 298 set into soil) flew and were released (*curve H3*). At about sunrise, 76 of the beetles remaining flew off (*curve H4*); a further 13 beetles then emerged and these beetles were kept in a cage where they continued to fly actively for up to 2 h after sunrise (not shown). The dusk crepuscular flights of *O. alexis* (*curve AX12*) and *O. fulgidus* (*F2*) coincided in time. The dusk flight of *O. uncinatus* began later and continued into the darkness of early evening (*curve U3*). The flight activity of *O. mendax* (*M5*) was predominantly at dawn during this flight trial, with some beetles flying during the night. This beetle, however, also flies at dusk. The apparent lull in dung beetle flight activity during the middle of the night is misleading, as in this area it is occupied by various coprine species, which are exclusively night-flying beetles. Sunset (*SS*) and sunrise (*SR*) times are marked by *arrows*

sunset (Fig. 4), and that dawn flight extended well into the morning, occasionally up to 2 h after sunrise.

Day-flying species

Several species of *Onitis* fly only in the daytime, such as the western Mediterranean species *O. belial* and *O. ion*, and autumn-active species *O. licitus* and *O. minutus* of the Western Cape Province, South Africa. Although we did not examine the diel flight behaviour of these species in detail, the small numbers of laboratory-reared specimens of *O. belial* and *O. ion* used flew only around noon in bright sunlight. *O. licitus* (body length 12–12.5 mm) and *O. minutus* (8–12 mm) are small autumn-active species that fly only during the day (A. Davis, personal communication), presumably partly because dusk and night-time air temperatures are too low to allow these small beetles to sustain flight at this time of the year (see below).
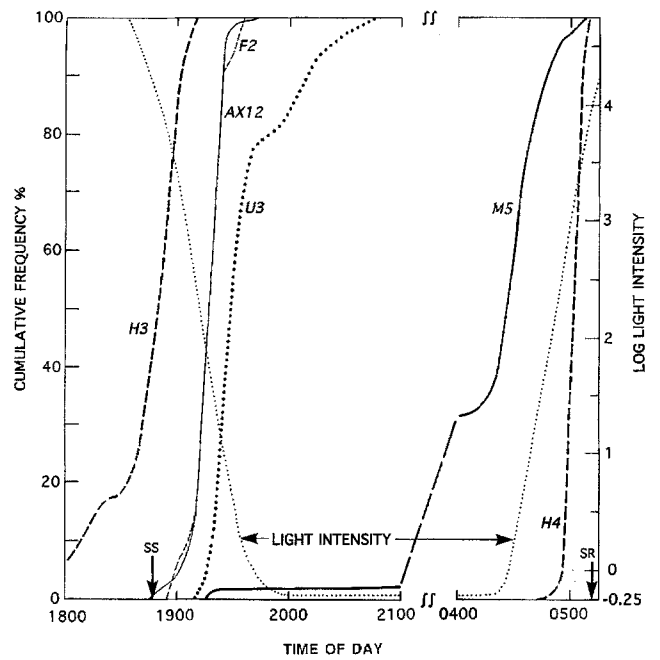
Pre-flight warmup in crepuscular-nocturnal dung beetles

The thoracic temperatures of onitine beetles resting beneath or crawling on the soil surface lies usually within 1 °C of the ambient soil or air temperature. In preparation for the onset of dusk or night flight, however, the thoracic temperature in *Onitis* spp. rises to between 35 °C and 40 °C. Figure 5 shows the extent of pre-flight endothermic warm-up in nine *Onitis* species, as well as the relative ability of three of these species to thermoregulate, i.e. maintain a constant thoracic temperature at lift-off over a range of ambient temperatures. The dusk flier *O. alexis*, which tends not to fly when soil (and air) temperatures fall below 17 °C (Houston and McIntyre 1985), is able to raise its thoracic temperature to about 34 °C when initiating flight just above this temperature limit (Fig. 5). Unlike larger
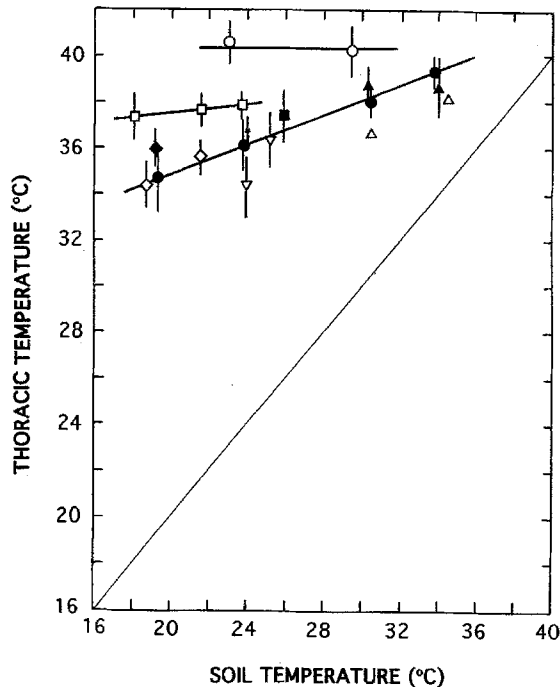
Fig. 5 Endothermic warm-up in preparation for flight in onitine dung beetles. The thoracic temperatures of nine *Onitis* species and *H. castelnaui* were measured immediately after the dusk or night-time onset of flight. Two large species, *O. aygulus* (□) and *H. castelnaui* (○) maintained a near-constant thoracic temperature over the ambient temperature range, whereas in the smaller species *O. alexis* (●) the ambient soil temperature influences more strongly the extent to which it is able to warm up before flight lift-off. Although this species is unable to regulate its pre-flight thoracic temperature fully, the temperature excess (the difference between thoracic and ambient temperature shown as the vertical distance between each data point and the diagonal thermoneutral line) remains large at low ambient temperatures. Other small to medium-sized (0.4–0.9 g) species (plotted as *points* only) also thermoregulate quite efficiently in preparation for flight, and include *O. caffer* (*), *O. tortuosus* (◆◆), *O. fulgidus* (△), *O. mendax* (▽), *O. picticollis* (▲▲), *O. uncinatus* (■) and *O. viridulus* (◇). The *points* are the means ± SD of four or more measurements on different beetles, except for the two *O. fulgidus* values, each of which is the average of two measurements

species, which are able to thermoregulate well over a wide range of ambient temperatures, the pre-flight thoracic temperature in this smaller species (body live weight, 0.36 ± 0.06 g, mean ± SD, $n = 40$) is strongly influenced by the ambient soil temperature. *O. aygulus*, a larger species (0.73 ± 0.16 g, $n = 18$), appears to thermoregulate more efficiently and is able to warm its thorax to at least 19 °C above the soil temperature (Fig. 5); it is able to fly when soil temperatures are as low as 12 °C (S. Caveney, unpublished work). The largest onitine species examined, *H. castelnaui* (2.77 ± 0.48 g, $n = 20$), has a constant pre-flight thoracic temperature of 40–42 °C over a wide temperature range, and is able to warm up its thorax to more than 17 °C above ambient before flying at dawn (Fig. 5).

Discussion

Sub-Saharan Africa has a particularly rich scarabaeine dung beetle fauna which radiated in response to the ready availability of mammalian herbivore dung. Despite its abundance, competition for dung (whether required for food or breeding) may be fierce and this has presumably contributed to species-characteristic dung preferences (type, consistency, age), as well as different foraging behaviours (Hanski and Cambefort 1991). Dung beetles feeding on herbivore dung can be broadly classified as smooth dung- (e.g. from cattle, buffalo and other artiodactyls) or coarse dung-feeders (e.g. from elephants, rhinos and equids). The beetles may partition the resource by removing a quantity of dung from dung pad (ball-rollers or telecoprids), by burying dung directly beneath the pad (burrowers or paracoprids) or by feeding and breeding within the pad (pad-dwellers or endocoprids). The African onitines are all paracoprids and are mainly "herbivore specialists" (Hanski and Cambefort 1991); some feed on smooth and others on coarse dung. They forage by day or night or during twilight, or for a short time during one of these periods [G. Tribe (1976) and G. Bernon (1981), cited in Doube (1991)].

Flight period and resource partitioning by onitine dung beetles

Dung is an ephemeral resource, dropped throughout the day by different mobile mammalian herbivores. Dung provides feeding, mating and oviposition sites and is the sole larval food source. The beetles that arrive first to colonize fresh dung rapidly consume, bury, disperse and/or spoil it, making it less attractive to beetles that arrive subsequently (Heinrich and Bartholomew 1979). These individuals are forced to continue foraging for later-voided dung. This intense competition for a limited resource has no doubt contributed to the evolution of flight behaviours that favour intraspecific encounters over interspecific ones among sympatric species of dung beetle. That is, in a biome, each dung beetle species flies for a limited and often different period of the day foraging for fresh dung. Our findings suggest that most African dung beetles of the tribe Onitini are crepuscular-nocturnal fliers, although the genus *Cheironitis* and a few species of *Onitis* do fly during the daytime. No onitine species examined flew exclusively at night. In Africa the nocturnal niche appears to be largely filled by dung beetles of the tribe Coprini, such as *Heliocopris* (Kingston and Coe 1977) and *Copris*. Most beetles active during the day are ball-rollers of the tribe Scarabaeini, Gymnopleurini and Sisyphini, or small endocoprid and larger paracoprid members of the tribes Onthophagini and Oniticellini.

Mammalian herbivores range extensively as they graze or browse. Consequently, dung beetle species with different flight behaviours and dung preferences colonize dung pads that are usually well-separated, and the various species become partitioned in space. Flight behaviour clearly contributes to reducing direct competition between day-active and crepuscular/night-active species, as these two groups of dung beetles are rarely encountered in the same fresh dung pad. Even individual species in groups that fly at more or less the same time of the day, such as dusk fliers or dawn fliers, may colonize different pads of dung because of slight differences in their median flight-onset times. Two onitine species that are attracted mainly to the coarse dung of megaherbivores provide an example. Under favourable climatic conditions, *O. mendax* and *H. castelnaui* are active only in elephant and rhinoceros dung in central and southern Africa. The time of flight in these two species coincides roughly with the times of the day when elephants are most actively feeding, namely in the late afternoon, around midnight and in the early morning (Owen-Smith 1988). Most elephant dung appears to be voided towards the end of this feeding period. We observed that elephant dung deposited in the early evening contained *O. mendax* alone, suggesting that the arrival of large numbers of this species during the night pre-empts subsequent colonization of these pads at dawn by *H. castelnaui*. Elephant dung deposited at dawn contained large numbers of both species, while that deposited in the early morning (i.e. after sunrise) contained only *H. castelnaui*. Clearly subtle shifts in flight onset and duration, in this case in two species that both fly at dawn, may result in the spatial and temporal partitioning of a shared resource. This would contribute to reducing interspecific competition and aid in mate recognition and selection. On the other hand, species such as *O. alexis* and *O. fulgidus*, which fly concurrently at dusk and which appear to prefer buffalo (and cattle) dung over that of the megaherbivores, arrive at the same dung pads and remain together buried under them the following day. The distinctive late afternoon-dusk flight activity of *H. castelnaui* (Fig. 4) resembles that of the ball-roller *Kheper laevistriatus*, which also frequents elephant dung (Heinrich and Bartholomew 1979).

Several of the *Onitis* species studied here have different patterns of seasonal activity. In the southwestern Cape, for instance, *O. aygulus* is active in the summer while *O. caffer* is predominantly active in the fall and winter (Davis 1993). Possible seasonal effects on daily flight activity were not examined in this study.

Facultative endothermy, vision and the time of flight

Many scarab beetles, including a night-flying dynastine (rhinoceros beetle) (Bartholomew and Casey 1977), day-flying ball-rollers (Bartholomew and Heinrich 1978) and dawn-flying melolonthines (Chown and Scholtz 1993), raise their thoracic temperatures endothermically to about 40 °C just prior to flight, and maintain this temperature while airborne. Dung scarabs have a high wing loading, and it appears that the thoracic musculature has to be warmed up before flight in order for the wings to beat at a frequency high enough to power lift-off (Bartholomew and Casey 1977; Josephson 1981).

Thoracic warm-up is particularly expensive in energetic terms to small beetles because of radiant heat loss, and the level of thoracic metabolism demanded for flight is not sustained during periods of terrestrial activity. The following sequence of observed and presumed behaviours takes place before flight in a relatively small dusk-active onitine such as *O. alexis*. At sunset, and in anticipation of flight, the beetle burrows up from deep in the soil and forms an open chamber just below the soil surface, where it rests, with its head exposed to the changing light conditions, for up to 30 min. During this time the intended flight is normally initiated (or aborted if the temperature is too low, in which case the beetle digs back into the soil). Pre-flight warm-up in a dusk-crepuscular dung beetle is initiated when the ambient light perceived by its eyes falls (or in dawn-crepuscular species, rises) to a species-specific threshold intensity. Warm-up takes between 5 and 10 min in scarab beetles (Bartholomew and Heinrich 1978; Bartholomew and Casey 1977; Chown and Scholtz 1993).

The presence of a short warm-up period in *O. alexis* can been inferred by experimentally manipulating the light levels at dusk. When *O. alexis* is exposed to artificially bright light at dusk, flight is inhibited; when the level is lowered abruptly to the range permitting flight, flight is initiated only after a 5-min delay and peaks after 10 min (Houston and McIntyre 1985). A similar delay is seen before the onset of flight in crepuscular noctuid moths (Dreisig 1980). During the pre-flight warm-up period, the elytra of an onitine scarab are raised slightly and the abdomen pumps rhythmically, as seen in other scarab beetles when active (Bartholomew and Casey 1977; Casey 1988). Since the abdominal spiracles in dung beetles are concealed beneath the elytra, this ventilatory behaviour presumably enhances the O_2 supply to the flight muscles during warm-up.

All onitine dung beetles examined, irrespective of whether they fly only at dusk, such as *O. alexis*, or during the night or at dawn (provided soil and air temperatures permit) are able to raise their thoracic temperatures to between 35 °C and 40 °C before becoming airborne. The energetic cost of endothermic regulation to dung beetles adapted to fly at dawn is presumably offset by the availability and exclusivity of fresh large-herbivore dung at this time.

The ability of endothermic insects to thermoregulate depends on size and this may explain some of the

observed flight behaviours. Bartholomew and Heinrich (1978) suggested that only insects weighing more than 2 g are able to thermoregulate with precision over a wide range of ambient temperature. Body temperature in endothermic insects of less weight is influenced by ambient temperature. Nevertheless, *O. alexis*, weighing as little as 0.3 g, maintains a relatively constant and high pre-flight thoracic temperature over a soil temperature range of 14 °C (Fig. 5). Perhaps residing in narrow burrows in the soil before flight lift-off reduces the problems of convective heat loss in small dung-beetles: these beetles emerge quickly from their burrows to fly. Although *O. alexis* is able to warm up endothermically and fly at air temperatures above 17 °C at dusk, it was not observed to fly at dawn, even when soil temperature and light conditions appeared favourable for take-off. There is no strong evidence to suggest that present-day competition from other dung scarabs has resulted in this asymmetric flight behaviour. We suspect that the problem of thoracic cooling has selected against dawn flying in smaller crepuscular species. Larger dawn-crepuscular and nocturnal species that frequent smooth dung, such as *O. aygulus* and *O. uncinatus*, are less restricted from flying at day-break by cool air temperatures.

Body size in onitine dung beetles is also positively correlated with the sensitivity of their compound eyes to light (P. McIntyre and S. Caveney, unpublished observations). Medium- to large-sized night- and/or dawn-flying species have large eyes with wide effective superposition apertures, necessary to see and avoid obstacles while flying *rapidly* in dim light. Day-flying onitines, such as *O. ion* and *Cheironitis* spp., are generally smaller beetles with smaller eyes having narrower superposition apertures and reduced sensitivity to light. Presumably these beetles do not normally fly at low light intensities because they cannot see sufficiently well to do so. Small body size, then, may restrict long-range flight in a crepuscular-nocturnal beetle in at least two ways: it limits the beetle's ability to sustain a high thoracic temperature during cool nights and dawns, and it limits the beetle's ability to see well enough to navigate while flying at night.

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