# Dung pad residence time covaries with male morphology in the dung beetle *Onthophagus taurus*

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**Abstract.** 1. The immigration and emigration behaviours of *Onthophagus taurus* were investigated in a combination of field and laboratory experiments to examine patterns of dispersal in this species.

2. On average, the mean proportion of major males immigrating to baited pitfall traps decreased significantly with time. In contrast, the mean proportion of minor males and females did not change with time.

3. The time taken to emigrate from a dung pad differed significantly among major males, minor males, and females. This difference arose because major males spent a significantly shorter period of time residing within the dung pad. On average, more than 50% of major males had emigrated from the dung pads after 30 h, some 4 h earlier than minor males and females.

4. When the effects of body size were controlled, major males with longer horns were shown to have longer wings. Because major males spend more time in flight, longer wings may be an adaptation to more frequent dispersal. Alternatively, longer wings in major males may compensate for the production of aerodynamically costly horns.

**Key words.** Dispersal, dung beetle, dung pad residence time, emigration, immigration, *Onthophagus taurus*, wing development.

## Introduction

Insects that live in heterogeneous environments frequently encounter the problem of covering areas and time periods that are unsuitable for breeding (Shapiro, 1970; Southwood, 1977; Solbreck, 1978). For a colonising species that utilises ephemeral resources for both feeding and reproduction, an effective dispersal mechanism is particularly important if new habitats are to be reached before the old ones are depleted (Shapiro, 1970). One commonly exploited ephemeral resource is cattle dung, and the microhabitat that is provided is often utilised by a number of dung beetle species (Hanski & Cambefort, 1991). The number of beetles residing in a dung pad frequently exceeds the carrying capacity, generating conditions of intense intra- and inter-specific competition (Ridsill-Smith, 1991). Under these conditions, evolutionary theory suggests that the dispersal of individuals between pads should evolve to maximise each individual's fitness. Ideally, males should distribute themselves in dung pads so as to

maximize their number of matings, however this will be influenced by differences in the competitive ability of the males involved (Parker & Sutherland, 1986). Because mature females procure resources in dung pads, females should distribute themselves so as to receive a sufficient quantity of dung to provision their offspring. Although dispersal in both sexes is likely to be density dependent, males and females are likely to employ different criteria when making their movement decisions (Hanski & Cambefort, 1991).

At present, a total of 55 exotic species of dung beetles has been introduced into Australia (Doube *et al.*, 1991). One of these species, *Onthophagus taurus* (Coleoptera: Scarabaeidae) has spread explosively throughout the southwest of Western Australia to become the most predominant summer active species in this region. Males of this species are dimorphic (Fig. 1), which arises from nonlinearities in the allometric relationship between horn length and body size (Fig. 2). Major males develop enlarged horns, whereas the horns of minors are greatly reduced in size or lacking altogether (Hunt & Simmons, 1997). Males belonging to this genus typically fight for access to breeding tunnels, and physically larger majors are competitively superior (Moczek, 1996; Emlen, 1997). Because minor males are unable to guard

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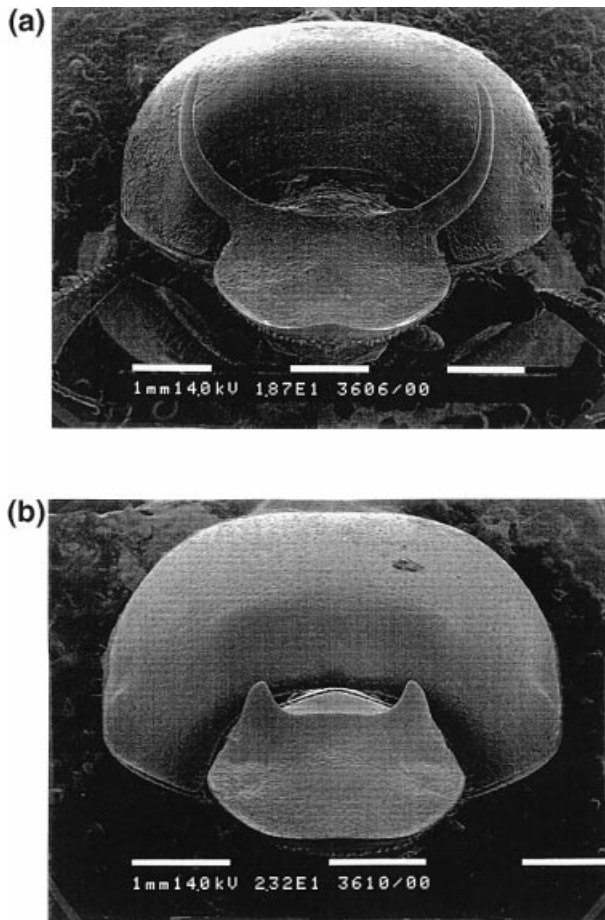
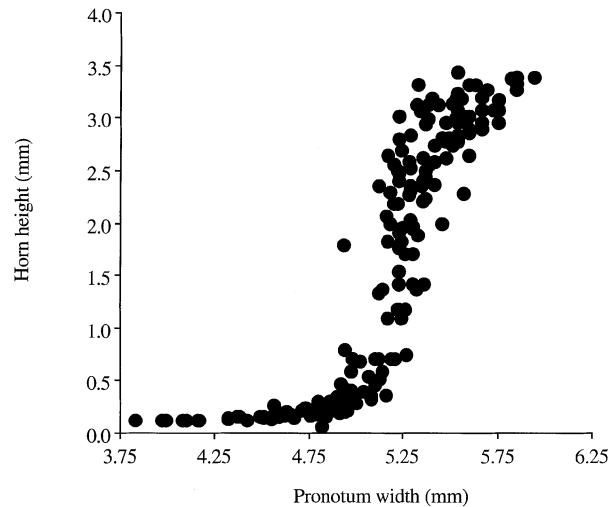Fig. 1. (a) A major male that guards a breeding tunnel, and (b) a minor male that *sneaks* copulations.



Fig. 2. The sigmoidal relationship between horn height and pronotum width in male *O. taurus*. Males switch to producing major horns at a pronotum width of 5.15 mm.

## Methods

### Reproductive biology of Onthophagus taurus

Adult *O. taurus* fly to fresh dung pads where they utilise dung for both food and reproduction. During reproduction, *O. taurus* bury portions of dung that have been removed from the dung pad, and pack them tightly into the blind end of a tunnel excavated beneath the dung pad. A single egg is then deposited into an egg chamber and sealed; one egg and its associated dung provision is referred to as a brood mass (Halfftner & Edmonds, 1982). Typically, the egg hatches after 2–3 days and the larva feeds on the dung provision. After ≈ 30 days of feeding, the larva constructs a pupal chamber with its own faeces and then pupates. The teneral adult remains within the pupal chamber for 2–3 days prior to emergence. Teneral adults emerge sexually immature, and require a feeding and maturation period before becoming sexually receptive (Halfftner & Edmonds, 1982). In south-western Australia, *O. taurus* emerge in large numbers in the summer, however the exact phenology remains largely unknown. Based on the phenology of *Onthophagus binodis* in this region (Ridsdill-Smith & Hall, 1984), it is likely that *O. taurus* completes at least two generations per year. Oviposition in *Onthophagus binodis* typically occurs when the peak abundance of beetles begins to decline in the field (September to November and February to April), and such factors as dung characteristics (Ridsdill-Smith, 1986), temperature, rainfall, soil conditions (Barkhouse & Ridsdill-Smith, 1986), and the density of beetles in pads (Ridsdill-Smith *et al.*, 1982) have been shown to influence oviposition behaviour. At the time of experimentation, female *O. taurus* were sexually mature, containing mature oocytes and producing fertile brood masses when maintained in the laboratory. It is not known

tunnels successfully, they adopt a tactic that involves sneaking undetected into tunnels past the guarding male or bypassing the major altogether by constructing smaller side tunnels (Emlen, 1997).

In the field, adults commonly reach densities exceeding 3000–5000 individuals per pad, with up to 80% of males representing the minor morph (J. Hunt, unpubl. obs.). Thus, competition for mates and larval resources can reach an intensity where an individual's fitness gains may be maximised by dispersing to a fresh pad. In particular, if the ability of a major male to guard a breeding tunnel successfully is hindered when the frequency of sneaks increases, major males would benefit by dispersing to fresh pads. In this paper the hypotheses that: (1) major males should leave dung pads more readily than minor males and females, and (2) major males should invest more heavily in wing development because they are likely to spend more time in flight were tested. To test these hypotheses, the immigration of beetles to baited pitfall traps in the field and the emigration of beetles from dung pads in the laboratory under natural morph frequencies and densities observed in the field, were examined.

whether females actually construct brood masses in the field at this time.

*Immigration experiment*

The immigration behaviour of *O. taurus* was studied in January 1998 at a cattle pasture in Margaret River (33°52′S, 115°05′E) in the south-west of Western Australia. Eight pitfall traps were spaced 7 m apart along a north–south transect line. Each pitfall trap consisted of a 40-cm high × 20-cm diameter plastic cylinder buried level with the soil surface, a 20-cm diameter funnel resting on top of the cylinder, and a 15-cm high × 10-cm diameter collecting vial housed within the cylinder and attached firmly to the bottom of the funnel. A 25-cm$^2$ piece of wire mesh (2 cm$^2$ grid) was placed on top of each funnel, and 500 g of fresh cow dung packed in a porous cloth bag was placed over the funnel to attract beetles. *Onthophagus taurus* fly between dung pads, and upon contacting the surface of the baited dung typically fell into the funnel and accumulated in the collecting vial. Pitfall traps were sampled every 20 min for a total of 3 h 20 min (10 sampling intervals). The beetles collected in each sample were placed independently in sealed bags and frozen prior to sorting in the laboratory. Frozen beetles were separated into males and females, based on the presence or absence of head horns, and males were further divided into majors and minors, based on the calculated pronotal switch point (see below). For each sampling interval, the number of individuals collected in each of these three categories was counted.

*Determination of the pronotal switch point*

To determine the pronotum width at which males switched from producing minor horns to major horns, horn height and pronotum width were measured for 190 males that were collected in pitfall traps. Horn height was measured for the left and right horns using an eyepiece graticule, and was taken as the vertical distance between the junction of the head and the tip of horn; the average height was used in analysis (see Hunt & Simmons, 1998b). The maximum width of the pronotum was measured using digital calipers. Pronotum width was used as a measure of body size. The pronotal switch point was calculated according to the statistical model of Eberhard and Gutiérrez (1991). Hunt and Simmons (1998b) provide a detailed outline of this procedure. *Onthophagus taurus* demonstrated a significant deviation from linearity between pronotum width and horn height ($\beta_2$: 46.52 ± 8.57, $t = 5.43$, d.f. = 189, $P < 0.001$) (Fig. 2). The pronotal switch point, explaining the greatest proportion of variance ($r^2 = 0.833$), occurred at a pronotum width of 5.15 mm. The dimorphism was characterised by a change in linear slope at the switch point ($\beta 2$: 2.37 ± 0.35, $t = 6.84$, $P < 0.001$), and a discontinuous distribution of horn lengths ($\beta 3$: 1.30 ± 0.12, $t = 10.70$,

$P < 0.001$). Males from this population could therefore be separated into two discrete morphs, with major males having a pronotum width of $\geqslant 5.15$ mm (Fig. 1a) and minor males having a pronotum width of $< 5.15$ mm (Fig. 1b).

*Emigration experiment*

Following the immigration experiments, pitfall traps were left for a further 90 min to collect a large quantity of beetles for the emigration experiments. The emigration behaviour of *O. taurus* was examined at the University of Western Australia campus under natural summer light and temperature regimes (LD 14 : 10 h, 30–35 °C) across eight independent beetle populations. Each population was established so that the density, morph ratio, and sex ratio accurately reflected natural levels observed in the field. The morph ratio in the field is typically four minor males per major male, and the sex ratio is 1 : 1 (derived from the immigration experiment), so each population of 300 beetles comprised 150 females, 120 minor males, and 30 major males. A 3-litre dung pad may contain up to 3000–5000 beetles in the field (J. Hunt unpubl. obs.). Each population was therefore given 250 g of dung. Each population and dung supply was placed in a 10-litre bucket containing moist sand. This bucket was then placed inside a 60-litre bucket and sealed with a nylon mesh cover. The bottom of the 60-litre bucket contained water so that beetles attempting to emigrate from the dung pad would hit the mesh cover, drop into the water, and become trapped. The water in each of the buckets was checked every hour beginning at 06.00 hours, and emigrating beetles were collected and assigned as minors, majors, or females. Emigration was measured as the time taken to leave the dung pad, and was expressed as the proportion of individuals still residing in the pad for each time interval. The emigration experiment lasted for a total of 60 h.

*Wing allometry*

Dung pad relocation in *O. taurus* depends on flight, so the level of investment in wing development was assessed for both male morphs. The left and right wings of 50 minor and 51 major males were mounted on microscope slides using transparent tape and measured using an eyepiece graticule in a binocular microscope. Wing length was taken as the distance between the junction of the wing to the abdomen and the outer margin of the second longitudinal vein. The average of the left and right wings was used in analysis. Horn height and pronotum width were measured as described above.

*Statistical analysis*

To examine the immigration behaviour of minor males, major males, and females, the mean proportion of beetles arriving at pitfall traps at each sampling interval was regressed against time. The proportional data was arcsin transformed to ensure that the data exhibited normality rather than a binomial
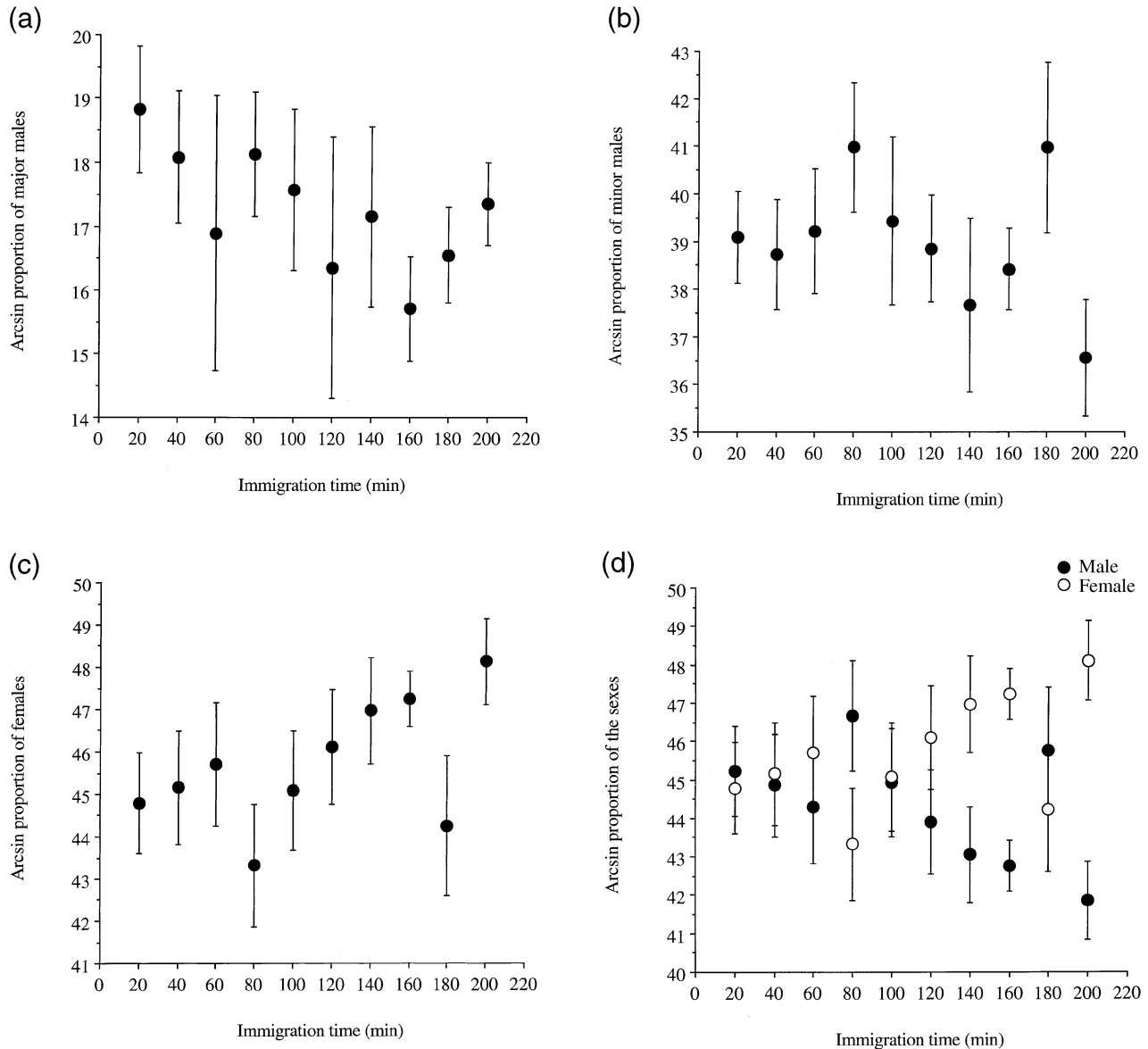
**Fig. 3.** The mean (± SE) arcsin proportion of (a) major males, (b) minor males, (c) females, and (d) males and females, immigrating to pitfall traps across each of the 10 sampling intervals.

distribution (Zar, 1984). The emigration behaviour of *O. taurus* was examined using a Kruskal–Wallis nonparametric analysis on the proportion of individuals residing in the dung pad at each time sampling interval, and for each of the eight replicates. A multiple nonparametric comparison with unequal sample sizes was used to locate the cause of differences in the Kruskal–Wallis analysis (Zar, 1984). Probability levels were Bonferroni adjusted for the multiple comparisons. A multiple regression analysis was used to examine the level of investment in wing development, where wing length was taken as the dependent variable.

## Results

### Immigration experiment

The mean proportion of major males immigrating to the pitfall traps decreased significantly with time (least squares regression: $F_{1,8}=6.56$, $n=10$, $P<0.05$) (Fig. 3a), however the mean proportion of minor males and females did not change with time (minors: $F_{1,8}=0.76$, $P=$NS; females: $F_{1,8}=3.34$, $P=$NS; $n=10$ in both cases) (Fig. 3b,c, respectively). Although there was a tendency for the proportion of males to

**Table 1.** Kruskal–Wallis analysis of the dung residence times of female, minor male, and major male *O. taurus*. F = females, Mn = minor males, and Ma = major males.

| Replicate | $\chi^2$ | $Q_{F-Mn}$ | $Q_{F-Ma}$ | $Q_{Mn-Ma}$ |
|---|---|---|---|---|
| 1 | 10.17** | 0.19 | 5.01*** | 6.13*** |
| 2 | 15.27*** | 1.32 | 5.62*** | 8.13*** |
| 3 | 11.92** | 1.21 | 5.95*** | 5.66*** |
| 4 | 2.64 | – | – | – |
| 5 | 9.62** | 1.52 | 5.07*** | 4.50*** |
| 6 | 22.65*** | 3.95*** | 6.90*** | 3.71*** |
| 7 | 6.25 | – | – | – |
| 8 | 1.29 | – | – | – |

** $P < 0.01$, *** $P < 0.001$ after Bonferroni adjustment.

decrease over time and the proportion of females to increase over time, these trends were not significant (males: $F_{1,8} = 3.35$, $P = NS$; females: $F_{1,8} = 3.34$, $P = NS$; $n = 10$ in both cases) (Fig. 3d). The overall sex ratio was $0.989 \pm 0.031$ males per female, and this did not differ from a 1 : 1 sex ratio ($\chi^2 = 3.02$, d.f. = 1, $P = NS$).

*Emigration experiment*

In five of the eight beetle populations, the time taken to emigrate from a dung pad differed significantly between major males, minor males, and females (Table 1). In all but one instance, this difference arose because major males spent a significantly shorter period of time residing within the dung pad than both minor males and females (Table 1, Fig. 4). This difference in the emigration rate was most pronounced in the first 6 h of the experiment. On average, more than 50% of major males had emigrated from dung pads after 30 h, some 4 h earlier than minor males and females (Fig. 4).

*Wing allometry*

Body size and horn size are correlated in *O. taurus* (Fig. 2), so a multiple regression was used to partial out the effect of horn size on wing size independent of body size. When the effects of body size were accounted for in the analysis, major males with longer horns were shown to have longer wings ($F_{2,48} = 42.14$, $P < 0.001$; body size: $0.46 \pm 0.12$, $t = 3.87$, $P < 0.001$; horn size: $0.104 \pm 0.03$, $t = 3.21$, $P < 0.01$; mean ($\pm$ SE) residual wing length = $-0.002 \pm 0.001$ (mm). There was no such pattern for minor males ($F_{2,47} = 206.09$, $P < 0.001$; body size: $0.77 \pm 0.08$, $t = 10.26$, $P < 0.001$; horn size: $t = 0.87$, $P = NS$; mean ($\pm$ SE) residual wing length = $0.002 \pm 0.001$ (mm).

**Discussion**

The results of this experiment demonstrate clearly that major males have a shorter dung pad residence time than both minor
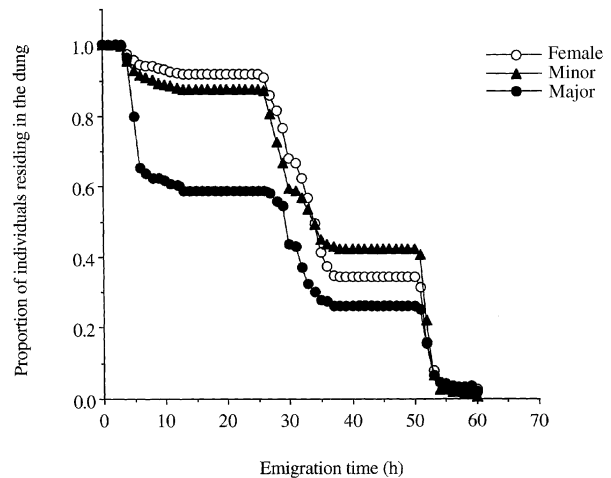


**Fig. 4.** The total proportion of major males, minor males, and females residing within dung pads for each time interval taken across the eight replicates.

males and females. The highest proportion of major males immigrates to dung pads immediately following deposition in the field, and upon reaching a pad they stay a significantly shorter period of time before emigrating. Sowig (1996) found similar differences in the emigration behaviour of males in another onthophagine species, *Onthophagus vacca*. In *O. vacca,* males can be classified as either resident or nonresident males depending on their emigration behaviour, with nonresident males typically leaving the dung pad within 60 h of arrival (Sowig, 1996). Sowig (1996) accounted for this difference in residence times between males as their inability to locate a receptive female rather than the fact that nonresident males may not have been willing to provide assistance during the construction of brood masses. Lawrence (1987) found that in the milkweed beetle (*Tetraopes tetraophthalmus*), small males emigrated from milkweed patches before large males when the sex ratio was male biased. In this instance, however, emigration between patches represents an alternative mating tactic, because the movement of small males from patches where they were at a competitive disadvantage resulted in an increased mating success (Lawrence, 1987). This seems unlikely in *O. taurus*, however, because major males are competitively superior, at least in paired encounters (Moczek, 1996). Nevertheless, before the dispersal patterns of majors can be dismissed as an alternative mating tactic, the reproductive success of majors that emigrate from a dung pad needs to be compared with the reproductive success of remaining majors.

One possible explanation for the elevated level of dispersal in major males may involve the relative costs of sperm competition between the male morphs. Parker's (1990) sperm competition game theory model for sneaks and guarders predicts that as the frequency of sneak matings increases in the population, the asymmetry in the risk of sperm competition between the two tactics should decline. In *O. taurus,* the increased encounter rate of the sexes at high pad densities

coupled with the predominance of sneak males in the population is likely to increase the risk of sperm competition to a level that is similar across the male morphs (Simmons *et al.*, 1998). Disparity in the costs associated with sperm competition between the morphs, however, should promote dispersal in the morph experiencing the greatest costs. One factor that is likely to influence the costs of sperm competition is the level of paternal care that is provided (Maynard Smith, 1977; Zeh & Smith, 1985). In *O. taurus*, major males typically assist females in larval provisioning while minor males do not (Hunt & Simmons, 1998a). Consequently, a major male that is cuckolded will lose the fitness benefits of his investment along with the opportunity for additional matings, whereas minor males will only experience a reduced certainty of paternity. While a number of beetle species are able to increase their certainty of paternity through a repeat-mating tactic that displaces the sperm of satellite males (Brussaard, 1983; Müller & Eggert, 1989; Lissemore, 1997), this tactic will only remain profitable until a threshold sneak frequency is reached (Maynard Smith, 1982). The dispersal of major males may reflect the point at which it no longer benefits a major to guard, but instead favours dispersal to a fresher dung pad.

Alternatively, the earlier emigration of major males from dung pads may reflect the lowered benefits associated with guarding a female under conditions of intense resource competition. Competition between dung beetles often leads to a reduction in the number of brood masses produced and/or the weight of brood masses produced (Holter, 1979; Ridsdill-Smith *et al.*, 1982). In *O. taurus*, increases in beetle density typically reduce the amount of dung provided to each brood mass (J. Hunt, unpubl. obs.), and thus offspring develop to a smaller adult body size (Hunt & Simmons, 1997). Because adult body size is a major determinant of both male (male competitive ability; Moczek, 1996) and female (potential fecundity; J. Hunt, unpubl. obs.) fitness in *O. taurus*, guarding a female when competition for resources is intense may not enhance the reproductive effort of a major male significantly. In this instance, it may be more profitable for a major male to disperse to a dung pad of lower density, and to guard a female that is able to provision offspring at a higher level. Minor males, on the other hand, have relatively less to lose by mating under conditions of intense competition, and thus may benefit by remaining at these high-density pads for a longer duration. Indeed, the reproductive success of minor males may even be enhanced through the early removal of competitively superior majors and the resulting skewed sex ratio that is produced. It is unclear why females may opt to spend longer at high-density pads. One possibility is that females are feeding at these pads rather than reproducing. This would require that females have some mechanism by which to gauge density and determine the point at which reproduction is no longer profitable and feeding should prevail.

Assuming that the time taken to locate a fresh dung pad in the field is equal between the male morphs, the shorter residence time exhibited by major males means that they spend more time flying. Therefore, the production of relatively longer wings by major males may represent an adaptation to the more frequent dispersal. Alternatively, if the production of large horns imposes an aerodynamic cost, the increased wing length of majors may compensate these costs. While secondary sexual trait compensation has been demonstrated convincingly in numerous bird species with elaborate tails (Hedenström & Møller, 1992; Andersson & Andersson, 1994; Balmford *et al.*, 1994) and aerodynamically costly sexual displays (Møller *et al.*, 1994), this study shows that secondary sexual trait compensation may have widespread implications in other nonavian taxa. It remains to be shown, however, that the horns of major male *O. taurus* impose a significant aerodynamic cost.

## Acknowledgements

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