Confidence of paternity and paternal care: covariation revealed through the experimental manipulation of the mating system in the beetle *Onthophagus taurus*

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Abstract

Theoretical models of paternal care predict that facultative reductions in male care may occur under certain conditions. One important parameter that has been shown to influence the outcome of these models is a male's confidence of paternity. In this study, we tested whether the amount of care provided by horned males in the dimorphic beetle, *Onthophagus taurus*, varied with his confidence of paternity. Male care results in an increased weight of dung provided in the brood masses produced by the pair. Using the sterile male technique we showed that a horned male's paternity declined with the number of sneak males in the population. The relationship was nonlinear, with paternity declining most rapidly between a frequency of one and three sneaks, and stabilizing thereafter at about 50%. A horned male's paternity was directly related to the number of copulations with the female, relative to the number of copulations achieved by sneaks. Horned males were shown to reduce their care in relation to their declining paternity. Video analysis demonstrated that reductions in male care occurred through a combination of male desertion and a trade-off between caring and paternity assurance behaviours. The number of fights with sneak males was negatively related to the amount of care provided by a horned male. These results suggest that by gauging his expected paternity through the number of fights with sneaks, a horned male is able to assess his paternity and reduce his investment accordingly. Our data thus provide strong empirical support for the proposed link between paternity and paternal care.

Introduction

According to Hamilton's rule ($rb - c > 0$), the evolution of parental behaviour should depend exclusively on the costs to the parents (c) and the benefits to the offspring (b), because the relatedness (r) between parent and offspring should be the same for all offspring and for both parents (Hamilton, 1964). However, sperm competition because of multiple mating by females can reduce the average relatedness between males and the young produced by their mates, and is a widespread phenomenon across animal taxa (Smith, 1984; Birkhead & Møller, 1998). Thus, males often face the uncertainty of investing in offspring to which they are not genetically related. Given that males cannot increase their fitness by investing in unrelated offspring, Triver's (1972) proposed that uncertainty of paternity would favour male desertion because failure to assure paternity prior to investment would put a male at a selective disadvantage in competition with more reproductively selfish individuals. Consequently, variation in a male's confidence of paternity has been proposed to explain the observed inter and intrasexual differences in the magnitude of paternal care provided (e.g. Ridley, 1978; Alexander & Borgia, 1979).

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Theoretical models have sought to establish the influence of confidence of paternity, the average probability that a male is the father of a given set of offspring (Alexander, 1974; also referred to as certainty of paternity; Maynard Smith, 1978, 1982), on the evolution of paternal care. The early models of Maynard Smith (1978) and Grafen (1980) concluded that as low confidence of paternity will, on average, have an equal effect across all breeding attempts, low confidence of paternity alone is insufficient to select against paternal care. These models assumed that paternity remains constant across all matings, that individuals are unable to assess their own level of paternity, and that the only cost of investment is the missed opportunities for remating. However, it has since been shown that by relaxing one or all of these assumptions, reduced confidence of paternity can select against the evolution of paternal care (Werren *et al.*, 1980; Winkler, 1987; Whittingham *et al.*, 1992; Xia, 1992; Westneat & Sherman, 1993). Indeed, Westneat & Sherman's (1993) analysis showed how the outcome of theoretical models can be highly variable, depending on how each of these assumptions are adjusted.

Empirical studies of the influence of paternity on paternal care have come predominantly from studies of birds. Some have reported positive associations between paternity and paternal care (e.g. Westneat, 1988; Lubjuhn *et al.*, 1993; Weatherhead *et al.*, 1994; Sheldon & Ellegren, 1998) whereas others have found no such relationship (e.g. Wright & Cotton, 1994; Westneat, 1995; Whittingham & Lifjeld, 1995). It is difficult to assess the general influence of confidence of paternity on paternal care from such studies because positive relationships can arise because of covariation between both variables and a third causal factor such as male quality, or because the experimental manipulations employed have failed to have their proposed affect on confidence of paternity (Schwagmeyer & Mock, 1993; Kempenaers & Sheldon, 1997; Wright, 1998). Thus, evidence that confidence of paternity can generate facultative variation in patterns of paternal care remains elusive (Wright, 1998).

Wright (1998) advocated a whole mating system approach to the study of paternity and paternal care. Westneat & Sherman's (1993) analysis concluded that confidence of paternity should favour the evolution of facultative paternal care. Their theoretical analysis was based on the trade-off between effort expended in obtaining matings and thus higher levels of paternity, effort expended in caring for offspring, and effort expended in somatic maintenance and thus future reproduction. Importantly, this approach links paternal care and paternity, not simply through the paternal effort function, but also through the trade-off between paternal effort and mating effort (Wright, 1998). Wright (1998) thus concluded that a better understanding of the link between paternal care and paternity could be attained through an integration of the research areas of sexual

selection and paternal care, and further, that experimental data on a wider range of taxa, more amenable to experimental manipulation of the mating system, were needed.

Parental care of eggs or young is typically rare among invertebrates (Clutton-Brock, 1991). However, in dung beetles belonging to the genus *Onthophagus*, biparental care is common (Lee & Peng, 1982; Cook, 1988; Sowig, 1996; Hunt & Simmons, 1998a, 2000; Moczek, 1999). During reproduction, members of this genus typically remove portions of dung from the pad and pack it into the blind end of tunnels constructed beneath the dung pad. A single egg is deposited into an egg chamber and sealed; one egg and its associated dung provision constitutes a brood mass (Halffter & Edmonds, 1982).

Many Onthophagine dung beetles exhibit dimorphisms in the male body plan, in which large 'major' males develop enlarged horns on the head and/or pronotum and small 'minor' males are hornless (Cook, 1987; Emlen, 1996; Hunt & Simmons, 1997, 1998b, 2000). A male's morphology is determined by a hormonal switch that governs his developmental pathway and is triggered by the amount of dung provisioned by his parents in the brood mass (Emlen & Nijhout, 1999). As such, the alternative phenotypes are discrete and are dependent on the environment provided by the parents (Hunt & Simmons, 1997, 2000).

Male dimorphisms in this genus are also associated with alternative mating tactics; horned males fight for access to females whereas hornless males sneak copulations with females that are being guarded by horned males (Emlen, 1997; Moczek & Emlen, 2000). Furthermore, studies examining patterns of parental care have shown that it is typically only the horned males that provide assistance during brood mass construction (Cook, 1988; Hunt & Simmons, 1998a, 2000; Moczek, 1999). In *Onthophagus taurus*, male provisioning commences with the production of head horns and represents an 'all-or-none' tactic with all horned males providing a fixed level of care (Hunt & Simmons, 2000). Provisioning by horned males results in the production of significantly heavier brood masses (Hunt & Simmons, 1998a, 2000) and as adult size is largely determined by the quantity of dung provided in the brood mass (Hunt & Simmons, 1997), paternal care has a substantial effect on the phenotype (Hunt & Simmons, 2000) and thus the future fitness of adult offspring (Hunt & Simmons, 2001).

Two features of the mating system of *O. taurus* may influence the probability that a horned male sires the young he provisions, and hence the fitness benefits associated with paternal care. First, females store sperm and mate with multiple males so that competition will exist between the sperm of different males to fertilize a given female's eggs (Tomkins & Simmons, 2000). Secondly, hornless sneaks can outnumber horned males by as much as 80% (Hunt *et al.*, 1999), so that horned males can have a high risk of being cuckolded. In

situations where confidence of paternity is low, selection should favour male desertion or at least reductions in his level of care (Westneat & Sherman, 1993).

Previously, Moczek (1999) has shown that paternal care in *O. taurus* is facultative. When in the presence of another male, horned males appear to reduce their level of care and increase their investment in mate-securing behaviours. Here we utilize this apparent plasticity in male behaviour to examine empirically the relationship between paternity and paternal care. We experimentally manipulate the mating system of *O. taurus* by varying the numbers of sneak males associated with a breeding pair. We quantify changes in confidence of paternity for horned males as sneak frequencies are varied, and how horned males respond to increasing sneak frequency in terms of the amount of dung they contribute to brood masses. Furthermore, we use video analysis to ascertain whether reductions in a horned male's care are the result of male desertion or whether increased guarding activities reduce the amount of care he is able to provide. We consider the implications of confidence of paternity in the evolution of paternal care in this species.

Materials and methods

General procedures

Onthophagus taurus were collected using baited pit traps from Margaret River in the south-west of Western Australia. Beetles were maintained for 2 weeks in a mixed laboratory culture with constant access to fresh cow dung to ensure that all beetles were reproductively mature and were mated. Three hundred females were established in individual breeding chambers (PVC piping, 25 cm in length and 6 cm in diameter), three quarters filled with moist sand and topped with 250 mL of cow dung, and left for a period of 1 week. Breeding chambers were then sieved and brood masses removed. Brood masses were buried in moist sand and reared through to adulthood. On emergence, the pronotum widths of males and females were measured using digital calipers and the horn lengths of males were measured using an eyepiece graticule with a binocular microscope.

Sneak frequency and confidence of paternity

We used the sterile male technique (Boorman & Parker, 1976) to examine the effect sneak frequency has on confidence of paternity for a horned male. Five sneak frequency treatments were examined with the number of hornless males varying from one to five housed with a single breeding pair. A total of 28 replicates were established for each of the sneak frequency treatments. In half of these, the horned male was irradiated and the sneaks remained fertile, and in the other half the sneaks were irradiated and the horned male remained fertile. Varying

frequencies of sneaks are likely to influence the numbers of matings a female has, which in turn could influence natural levels of fertility. Therefore, natural levels of fertility and sterility for females exposed to fertile and irradiated males were assessed in a further 10 replicates per sneak frequency treatment, half where all males were irradiated and half where all males were fertile. Males were sterilized using 11 Krads of gamma radiation from a cobolt-40 source. Preliminary experiments found that this dosage was optimal for this species; 99.11 ± 0.89% of eggs fertilized by sperm from irradiated males failed to hatch but the dose had no impact on male viability for the first 5 days following irradiation, or on their ability to court females and obtain matings (Hunt & Simmons, 2001).

Following irradiation, each horned male was paired with a randomly selected virgin female and placed in a small plastic container (9 × 9 × 5 cm) that was three quarters filled with moist sand and topped with 10 mL of cow dung. The pairs were left for 1 day to ensure that mating took place. On the second day, pairs were placed in an independent breeding chamber (PVC piping, 25 cm in length and 6 cm in diameter), three quarters filled with moist sand topped with 250 mL of cow dung, and maintained for 1 day. This enabled pairs to establish breeding tunnels and start provisioning brood masses. Thus, introduced sneaks would have to compete against a horned male that was actively defending a female's breeding tunnel. On the third day, sneak males were added to the breeding chambers. At the end of the fifth day, breeding chambers were sieved and brood masses collected. The chambers were re-established for an additional week with only the female present. At the end of this week, chambers were sieved and brood masses collected. Brood masses from both periods were maintained for 4 days at 25 °C and then scored as fertile or sterile to assign paternity. Paternity was calculated as the proportion of all eggs fertilized by fertile or sterile males. Proportions were arcsine transformed for statistical analysis, although raw proportions are presented for ease of interpretation.

This experimental design permitted a horned male–female pair to produce brood masses undisturbed by sneaks for a 1-day period. As a result, a proportion of brood masses produced in the first 5 days of the experiment are expected to be sired exclusively by the horned male. To correct for this, 20 pairs were established in independent breeding chambers where half of the horned males were irradiated and half where they were fertile, and maintained for 1 day. Chambers were then sieved and brood masses counted. The mean number of brood masses produced by these pairs (2.35 ± 0.25 brood masses) was subtracted from those sired by the horned males over the first 5 days of the experiment so that a horned male's paternity was not inflated.

We selected males for this experiment from the extremes of the pronotum width-horn length distribution
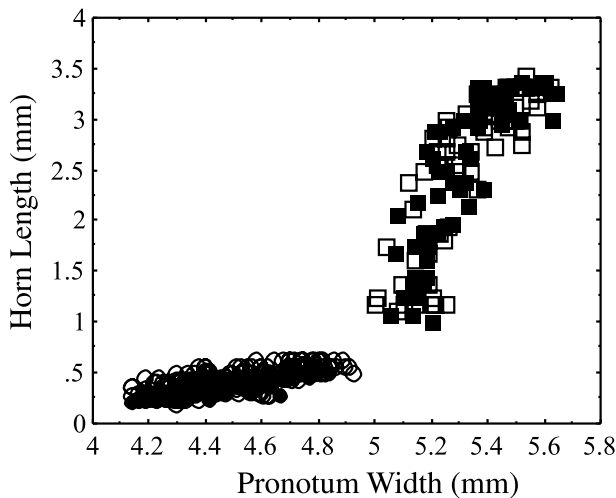
Fig. 1 The scaling relationship between pronotum width and horn length for male *O. taurus* used in the experimental examination of the relationship between sneak frequency and paternity. Horned (squares) and 'hornless' (circles) males were selected, so they differed significantly in both horn morphology and body size (*horn*: $F_{1,558} = 2781.3$, $P < 0.0001$; *pronotum*: $F_{1,558} = 3510.5$, $P < 0.0001$). Note that hornless males have a rudimentary horn the length of which is also measured. Males were randomly selected from these classes and allocated to the sneak frequency treatments, with half in each treatment being irradiated (open symbols) and half remaining fertile (solid symbols). The size of horned males and the mean size of hornless males did not differ significantly across the sneak frequency treatments, the irradiation sequence treatments, and there was no significant interaction (*F*-values ranged from 0.48 to 2.02, all *P*-values n.s.). Likewise, female body size did not differ significantly between the sneak frequency treatments they were assigned to, across irradiation sequence of the males she was paired with, and there was no significant interaction (*F*-values ranged from 0.44 to 3.04, all *P*-values n.s.).

(Fig. 1). Males were then randomly selected from these horned and hornless classes so that the sizes of horned and hornless males was random with respect to the sneak frequency treatments and the sequence of irradiation treatments (Fig. 1). Likewise, females were chosen at random so that female size did not differ between sneak frequency treatments, or between irradiation order treatments (see Fig. 1).

Sneak frequency and levels of paternal care

The same five sneak frequency treatments were used to examine the influence of varying numbers of sneaks on paternal care. A total of 14 replicates were established for each of the sneak frequency treatments. A horned male was randomly paired with a virgin female and placed in an independent breeding chamber, three quarters filled with moist sand and 250 mL of cow dung, and the pair left to breed for 1 week. Chambers were then sieved and brood masses collected. Chambers

were re-established for a second week of breeding in which we added the corresponding number of sneak males. At the end of the second week, breeding chambers were again sieved and brood masses collected. Fourteen replicates were established as controls, in which only the horned male was present in both weeks. In both weeks, excess sand was removed from brood masses using a dissecting probe and the brood masses were dried to constant weight at 60 °C. After drying, any remaining sand was removed and all brood masses were counted and weighed to the nearest 0.01 mg. Males and females were selected for this experiment as described above and in Fig. 1.

Behavioural analysis

To determine the proximate causes of changes in the care provided by horned males, we observed their provisioning behaviour using glass 'ant farms'. Provisioning behaviours were examined both in the absence of sneaks and when one or three sneak males were present during breeding. These treatments were selected as they encompassed the complete range of confidence of paternity experienced by a horned male during provisioning (see Results). Ant farms were constructed from two sheets of 0.5 mm glass (215 × 130 mm) separated by two glass strips (200 × 15 mm) along their length and a single strip along their width (130 × 15 mm). A single strip (130 × 15 mm) was used to seal the entrance once beetles had been added. Ant farms were held together using four alligator clips along their length and were mounted in wooden bases for stability. This design created a sealed internal chamber with a dimension of 200 × 100 mm for observations.

Each ant farm was three quarters filled with moist sand and topped with 50 mL of fresh cow dung. A single randomly selected virgin female was added to each chamber. Once a breeding tunnel was constructed and the female had started provisioning a brood mass, a single horned male was introduced into the tunnel. Once paternal assistance was observed, the corresponding number of sneak male(s) were added to the chamber and recording started. Provisioning behaviour was recorded using a time lag video recorder (Sony SVT 124P, Tokyo, Japan) via a Sony CCT video camera (XC-999P) fitted with a wide angle lens (VCL-03S12XM). All recordings were made under dim lighting in a constant temperature room at 25 °C. Each recording was made for the entire duration required to produce a single brood mass, a process that may take up to 14 h (Hunt & Simmons, 2002). Thus, all recordings were made at a tape speed of 10 frames s^{-1}. Our sampling regime contrasts that used by Moczek (1999) where male behaviour was examined for only three 30-min sampling periods over a 24-h period. We have shown that the level of care provided by horned males varies consistently through the breeding cycle so that spot sampling may not

accurately reflect the true levels of care provided by males (Hunt & Simmons, 2002). A total of five replicates were recorded for each of the three sneak frequency treatments. At the completion of recording, the constructed brood mass was removed from the observation chamber, dried, excess sand removed with a dissecting probe, and weighed to the nearest 0.01 g.

The behaviours performed by a horned male during offspring provisioning can be broadly categorized as either paternal effort or mating effort. Paternal behaviours were collectively described as cooperative because these contributed to the production of the brood mass and included: *Removing*, the male separates a small portion of dung from the pad; *Carrying*, the male carries a portion of dung to the brood chamber; *Packing*, the male packs dung into the blind end of the brood chamber; *Gathering from pad*, the male moves from the brood chamber to the pad to remove a portion of dung; and *Gathering from tunnel*, the male moves from the brood chamber to collect a portion of dung stored in the tunnel. In contrast, behaviours associated with mating effort do not benefit the offspring but rather constitute behaviours that increase a male's paternity. Such behaviours were collectively described as noncooperative and included: *Patrolling*, the male moves up and down the tunnel without collecting or carrying portions of dung; *Guarding*, the males remain motionless at the entrance to the breeding tunnel, or at the entrance to the brood chamber where the female is provisioning, or are engaged in aggressive interactions with sneaks; *Interacting with female*, including head to head interactions within the tunnel, courtship and mating. A male was assumed to have deserted his mate if, after mating, he left the breeding tunnel and did not associate with the female during the provisioning of the brood mass.

Each tape recording was analysed and the proportion of time spent in each behaviour was recorded to standardize for differences in the overall time taken to produce a brood mass.

Results

Sneak frequency and confidence of paternity

In our control treatments where all males were irradiated there was no significant influence of sneak frequency on the proportion of eggs that hatched ($F_{4,20} = 0.42$, n.s.) which averaged 0.02 ± 0.01 across all treatments. Similarly, where all males were fertile, there was no influence of sneak frequency on the proportion of eggs that hatched ($F_{4,20} = 0.48$, n.s.) which averaged 0.97 ± 0.01 across all treatments.

The proportion of eggs fertilized by irradiated sperm in each experimental replicate was calculated as $P_R = 1 - [(x - z)/(p - z)]$ where x was the observed proportion of brood masses containing viable eggs, z was

the proportion of viable eggs produced when all males were irradiated and p was the proportion of viable eggs produced when all males were fertile (Cook *et al.*, 1997). When the horned male was irradiated P_R gave his fertilization success relative to the fertile sneaks. When the horned male was fertile, his fertilization success was $1 - P_R$. Values less than or greater than 1 can be generated when $z > x$, so we corrected the data according to Cook *et al.* (1997).

The paternity data were analysed using a two-factor ANOVA with sneak frequency treatment and irradiation sequence (horned-fertile or horned-sterile) as main effects. There was a significant effect of the number of sneaks on a horned male's paternity ($F_{4,130} = 21.448$, $P < 0.0001$) (Fig. 2) but there was no significant irradiation effect ($F_{1,130} = 1.257$, n.s.) and no significant interaction ($F_{4,130} = 2.068$, $P = 0.09$). The ability of a horned male to protect his paternity against sneak males was nonlinear, declining most rapidly between one and three sneak males and then stabilizing beyond this sneak frequency (Fig. 2).

To determine if a horned male's paternity was influenced by his phenotype, we further analysed the data using an ANCOVA with the number of sneak males as the main effect, a horned male's pronotum width as the covariate and the horned male's paternity as the dependent variable. A horned male's paternity was significantly related to the number of sneak males present ($F_{4,130} = 20.49$, $P < 0.0001$) but was not related to the pronotum width of the horned male ($F_{1,130} = 0.73$, n.s.). Qualitatively similar results were attained if horn length was used instead of pronotum width (number of sneaks: $F_{4,130} = 20.29$, $P < 0.0001$; horn length: $F_{1,130} = 0.76$, n.s.).
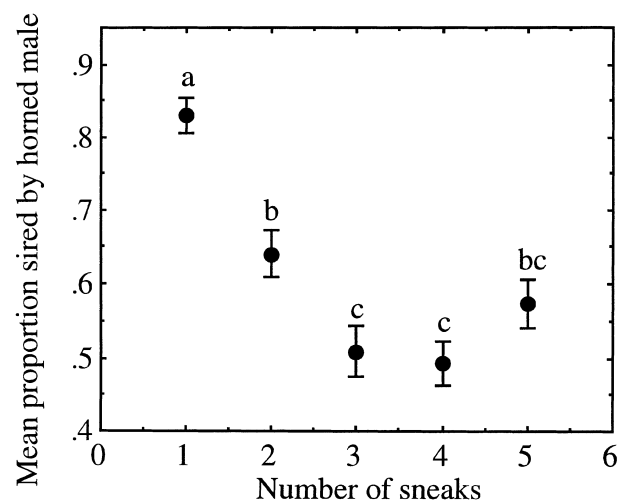

Fig. 2 The relationship between sneak frequency and the proportion of offspring sired by the horned male. Treatments with different letters differ significantly at $P < 0.05$ (LSD test).

Sneak frequency and levels of paternal care

Brood mass weight

We have shown elsewhere that brood mass weight decreases to a value predictable from female provisioning alone when paternal provisioning is experimentally removed (Hunt & Simmons, 2000). We examined the influence of sneak frequency on paternal care by looking at the change in the weight of brood masses produced after sneak males were added (weight of broods in week 1 − weight of broods in week 2) and assume that any change in brood mass occurs because horned males cease to provision, an assumption supported by our behavioural data below. There was a significant effect of sneak frequency on the change in weight of brood masses produced across weeks ($F_{5,82} = 7.69$, $P < 0.0001$) (Fig. 3). Pairs exposed to sneak males in week 2 showed a reduction in brood mass weight, while control pairs showed no change in brood mass weight between weeks 1 and 2 (Fig. 3). The reduction in brood mass weight was nonlinear, with the greatest decline in brood mass weight occurring between zero to three sneaks and then stabilizing beyond this sneak frequency (Fig. 3).

Brood mass number

There was a significant effect of sneak frequency on the change in number of brood masses produced across weeks ($F_{5,82} = 5.72$, $P < 0.001$) (Fig. 4). When exposed to sneak males, pairs showed a linear reduction in the number of brood masses produced, while control pairs tended to produce more brood masses in week 2 (Fig. 4).
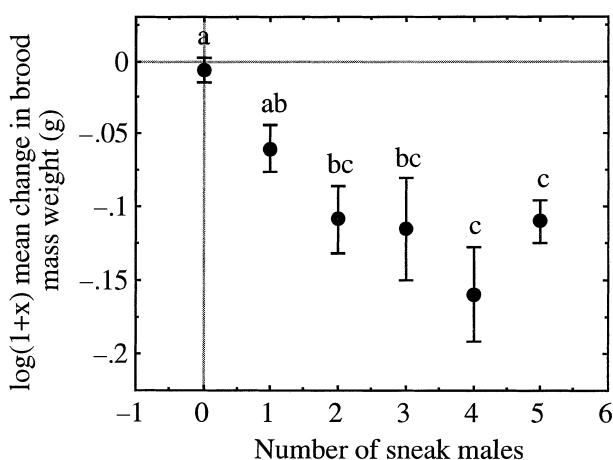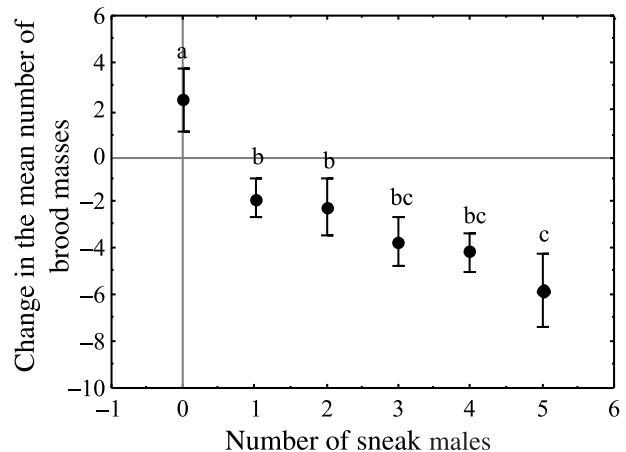

Fig. 4 The relationship between sneak frequency and the number of brood masses produced by a horned male–female pair. Treatments with different letters differ significantly at $P < 0.05$ (LSD test).

Behavioural analysis

Rates of desertion by horned males

There was a significant effect of the number of sneaks on the rate of desertion by the horned male ($\chi_2^2 = 8.74$, $P < 0.01$). Only one of six horned males deserted in the control treatment (16.67%), whereas 14 of 19 deserted in the single sneak treatment (73.68%) and 18 of 23 in the three sneak treatment (78.26%). The rate of desertion in both the single sneak ($\chi_1^2 = 7.77$, $P < 0.01$) and three sneak treatments ($\chi_1^2 = 8.52$, $P < 0.01$) were significantly higher than in the control treatment, but did not differ between the single and three sneak treatments ($\chi_1^2 = 1.19$, n.s.).

Behaviour of nondeserting horned males

For horned males that did not desert their mate, we analysed the proportion of time they spent performing cooperative (paternal care) and noncooperative (mating effort) behaviours using a linear discriminant analysis. The first canonical discriminant function explained 98% of the variance and significantly classified the data into control and sneak treatment groups (Wilks' $\lambda = 0.036$, eigenvalue = 18.794, d.f. = 14, $P < 0.01$). The second function explained the remaining 2% of variance and was of little importance in discriminating between these groups (Wilks' $\lambda = 0.72$, eigenvalue = 0.388, d.f. = 6, n.s.). The standardized canonical discriminant functions show that when exposed to sneaks, horned males increased the proportion of time spent guarding females and decreased the proportion of time spent provisioning the brood mass (Table 1). Conversely, in the absence of sneaks horned males increased the proportion of time spent provisioning and decreased the proportion of time spent guarding. As such there was a significant negative relationship between a horned male's score on

Fig. 3 The relationship between sneak frequency and the change in the mean weight of brood masses produced by a horned male–female pair. Treatments with different letters differ significantly at $P < 0.05$ (LSD test).

Table 1 Structure matrix for the discriminant function analysis of the influence of sneak frequency on provisioning behaviours of horned males.

Behaviour	Function 1
Guarding	0.778*
Packing	−0.529*
Removing	−0.351*
Interacting with female†	−0.104
Patrolling	−0.233
Gathering from pad	−0.245
Gathering from tunnel	−0.139
Carrying	−0.176

*Largest absolute correlation between each behaviour and any discriminant function.

†This behaviour not used in the discriminant analysis because it failed the tolerance test at a minimum tolerance level of 0.001.

discriminant function 1 and the weight of the brood mass produced by the pair; pairs produced significantly heavier brood masses in the absence of sneak males ($F_{1,14} = 29.80$, $P < 0.0001$) (Fig. 5).

Not surprisingly, the total number of matings by sneak males increased significantly with the number of sneak males present ($F_{2,14} = 12.60$, $P < 0.01$) (Fig. 6). Likewise, the total number of matings by horned males also increased significantly with increasing sneak frequency ($F_{2,14} = 4.67$, $P < 0.05$) indicative of retaliatory copulations in the presence of sneak males (Fig. 6). However, the proportional number of matings by a horned male decreased with increasing sneak frequency ($F_{1,14} = 8.20$, $P < 0.01$; control = 100%, one sneak = 70 ± 12.2%, three sneaks = 55.3 ± 6.3%) in qualitative and quanti-

Fig. 6 The mean (±SD) number of matings by horned (open bars) and sneak males (closed bars) in each of the sneak frequency treatments.

tative agreement with the negative relationship between paternity and sneak frequency seen in Fig. 2. It is noteworthy that in all cases where matings were observed, the horned male was the last male to mate with the female prior to egg deposition (14 / 14, binomial probability $P < 0.0001$). In one of the control treatments we did not observe mating during recording, but assume the pair had mated prior to the onset of provisioning which is when recording started.

A multiple regression using the number of matings attained by a horned male and the number of fights with intruding sneak males against brood mass weight showed that the level of care provided by a horned male was significantly reduced as the number of fights with intruding sneak males increased ($\beta = 0.41 \pm 0.12$, $t_2 = 3.31$, $P < 0.006$) but was unrelated to the number of matings he attained with a female ($\beta = -1.34 \pm 1.88$, $t_{14} = 0.71$, $P = 0.49$). Thus, by assessing the number of fights with sneak males, a horned male seems able to gauge his confidence of paternity and adjust his investment accordingly.

Discussion

In this study we provide clear evidence of a link between paternity and paternal care in the biparentally caring dung beetle *O. taurus*. The level of care provided by a horned male was related to the probability of siring offspring. Video analysis demonstrated that the reduction in care with declining paternity occurs through a combination of direct and indirect behavioural mechanisms. As a male's confidence of paternity decreased, he was more likely to desert his mate, or if he remained, a greater proportion of his time budget was directed towards paternity assurance leaving relatively less time available for parental duties.
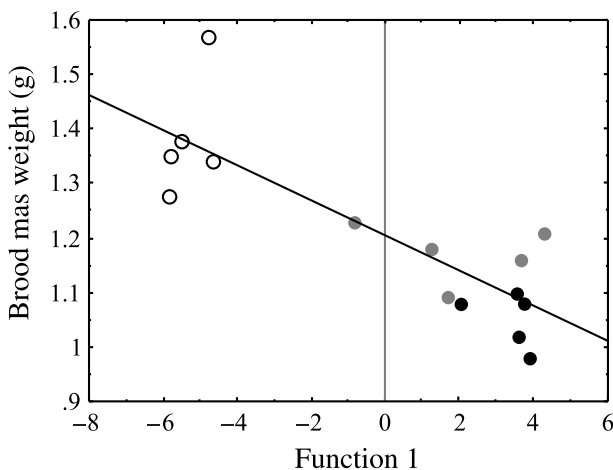

Fig. 5 The relationship between discriminant function one, which is directly related to the proportion of time spent providing care, and the weight of brood masses produced. Open circles represent horned males when no sneak males are present, the grey circles when one sneak male is present and the dark circles when three sneak males are present.
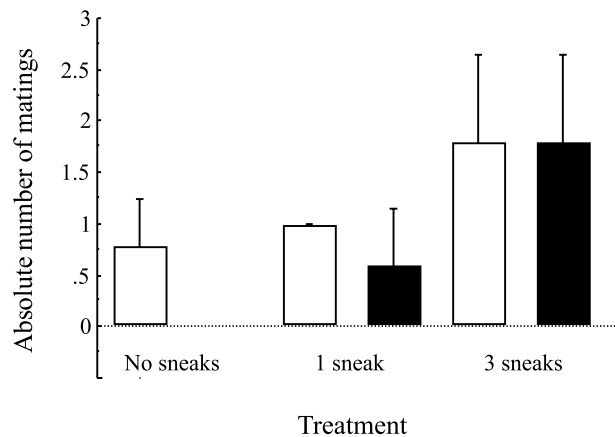
Confidence of paternity

Tomkins & Simmons (2000) found that when a female mates with just two males, sperm competition conforms to a mechanism of random sperm mixing so that each male obtains half of the offspring produced by the female. The results presented here suggest that this pattern of sperm utilization changes little with more extensive multiple mating. Females mated one to two times when one sneak was present and between two and six times when three sneaks were present. The fertilization success of horned males declined from an average of 83% with one sneak to 50% with three sneaks. These figures provide a close fit to our behavioural observations which showed a horned male's relative share of copulations declined from 70% when one sneak was present to 55% when three sneaks were present. Thus a male's share of fertilizations was proportional to his share of copulations. The presence of increasing numbers of sneaks decreases a male's relative share of copulations and his confidence of paternity.

We found that the absolute numbers of copulations performed by horned males increased with increasing sneak frequency. Studies of birds have found that males will perform retaliatory copulations following copulations by extra-pair males (reviewed in Birkhead & Møller, 1992) and Parker's (1990) theoretical models of ejaculation strategies predict that males should increase their ejaculate size in copulations following a detected sneak copulation. Such tactics should function in protecting a male's paternity in the face of sneak copulations. Our data show that in the highest sneak frequency, on average a horned male was able to match the copulation frequency of sneaks and obtained half of the fertilizations. This suggests that males do not increase the size of their ejaculate in retaliatory copulations. If they had, we would have expected them to obtain relatively more fertilizations than expected for their copulation frequency. Interestingly, males were found to adjust their levels of paternal provisioning in relation to the number of aggressive interactions with sneak males, rather than their absolute number copulations with the female, suggesting that encounter rate with sneaks, which will increase with sneak frequency, may represent a more reliable cue to confidence of paternity.

Theoretically, reduced paternity will have different effects on paternal care depending on the extent to which paternity varies between breeding attempts and whether or not this variation is predictable (Whittingham et al., 1992; Westneat & Sherman, 1993). Paternity should only influence paternal care if it is variable and either predictable, so that males evolve a behavioural response over evolutionary time, or if it can be directly assessed to allow facultative adjustments within a given breeding attempt (Maynard Smith, 1978; Grafen, 1980; Werren et al., 1980; Winkler, 1987; Whittingham et al., 1992; Xia, 1992; Westneat & Sherman, 1993). Indirect cues to

confidence of paternity have been assumed for a number of experimental studies of birds, and have included such cues as male age (Morton et al., 1990), time away from the female during her fertile period (Hatchwell & Davies, 1990; Koenig, 1990) and both the absolute (Møller, 1988, 1991; Burke et al., 1989; Davies et al., 1992) and relative number of copulations (Møller, 1988, 1991). However, despite the large number of paternity studies in birds, with few exceptions (Burke et al., 1989; Davies et al., 1992), information relating to the reliability of these cues in predicting paternity is still unavailable (see Wright, 1998 and references therein). Therefore, in many cases it is difficult to ascertain whether the experimental technique being used to manipulate a male's confidence of paternity is appropriate or even effective (Schwagmeyer & Mock, 1993; Kempenaers & Sheldon, 1997; Wright, 1998). This was not the case in our study of *O. taurus*. Experimental manipulation of sneak frequency had a clear effect on confidence of paternity and males adjusted their provisioning in relation to the numbers of encounters they had with sneak males.

Paternity and paternal care

The findings of this study contribute to an extensive list of empirical studies targeting the relationship between paternity and paternal care, but represent one of the first to target a taxa other than birds and to utilize an experimental manipulation of the mating system (Wright, 1998). Empirical studies on a number of bird species have claimed to show that males facultatively reduce their level of care in response to a lowered paternity (Møller, 1988; Møller & Birkhead, 1991, 1993; Davies et al., 1992; Dixon et al., 1994; Weatherhead et al., 1994; Wright & Cotton, 1994; Freeman-Gallant, 1996; Lifjeld et al., 1998). However, other studies demonstrate no such effect (Lifjeld et al., 1993; Stutchbury et al., 1994; Westneat, 1995; Westneat et al., 1995; Whittingham & Lifjeld, 1995; Dunn & Cockburn, 1996; Yezerinac et al., 1996; Birks, 1997). Likewise, comparative studies across bird species have provided both support for (Møller & Birkhead, 1993; Møller & Cuervo, 2000) and against (Schwagmeyer et al., 1999) a role for paternity in the evolution of paternal care.

There are a number of reasons why these earlier studies have proved equivocal. A link between paternity and paternal care can arise as a result of covariation with male phenotype. Males may, for example, vary in their phenotypic quality. Poor quality males may be unable to guard their mates effectively and thereby suffer higher levels of sperm competition than males of high quality. If phenotypic quality also influenced a male's ability to provide care, a link between paternity and paternal care would arise, although paternity itself had no causal influence on paternal care (Kempenaers & Sheldon, 1997; Wright, 1998).

In birds, females have been shown to be more likely to engage in extra-pair copulations and produce extra-pair young when paired with males having relatively unattractive secondary sexual traits (e.g. Smith, 1988; Norris, 1990; Kempenaers *et al.*, 1992; Graves *et al.*, 1993; Hasselquist *et al.*, 1995). Thus, unattractive males are likely to have a low confidence of paternity compared with attractive males, and this is unlikely to vary between breeding attempts. Under such conditions, a relationship between paternity and paternal care is not expected (Maynard Smith, 1978; Grafen, 1980; Westneat & Sherman, 1993). Moreover, unattractive males have actually been found to invest more in paternal care than attractive males, because they have lower opportunities to invest in extra-pair mating activity (Møller & Thornhill, 1998). Thus, it is perhaps not surprising that studies of birds have yielded such conflicting results given that in general they have not accounted for potentially confounding variables associated with the mating system of the species under study (Kempenaers & Sheldon, 1997; Wright, 1998).

In our study we compared the care provided by individual males under experimentally induced conditions of high and low confidence of paternity, thereby controlling for potentially confounding differences between males in phenotypic quality. Horned males were more likely to desert a female when sneaks were added to a breeding chamber, or if they remained, they reduced their level of provisioning. Two of the studies of birds that have supported a link between paternity and paternal care also observed changes in paternal care across breeding episodes of the same pair (Dixon *et al.*, 1994; Freeman-Gallant, 1996). Moreover, although body size and horn length are significant predictors of the competitive success of horned males (Moczek & Emlen, 2000), our data showed that in the context of our experiments, paternity was not dependent upon either body size or horn length. We have shown elsewhere that the level of male care is similarly independent of male phenotype (Hunt & Simmons, 2000) so that the link between paternity and paternal care demonstrated here cannot be explained by phenotypic variation between males.

An important result of our study is that we found the trade-off between paternal care and mating effort that is thought necessary for a link between paternity and paternal care (Westneat & Sherman, 1993). The proportion of a male's time budget spent provisioning offspring was inversely related to the proportion of time spent mate guarding and copulating with the female. The addition of sneaks into a breeding chamber thus resulted in males reducing the proportion of time they spent provisioning offspring and increasing the proportion of time they spent mate guarding. In an independent study of the same species, Moczek (1999) similarly found a switch from cooperative to noncooperative behaviour when a single male competitor was added to a breeding chamber.

Costs and benefits of extra-pair copulations

The results of this study lead to the obvious question, why do females mate with sneak males? Within a species, the prevalence of extra-pair copulations will depend on the costs and benefits of the female behaviour and on the efficiency of male counter strategies to avoid losing paternity (Westneat, 1995). Therefore, the occurrence of extra-pair copulations by females may often be viewed as the outcome of intersexual conflict, with the caring male attempting to control the mating behaviour of the female and the female evolving mechanisms to conceal such behaviour (Gowaty, 1996). In *O. taurus*, extra-pair copulations are not forced as the female must willingly open her genital tergite in order to mate. Therefore, it is possible that females may actively mate with hornless sneaks to derive genetic benefits for her offspring. Support for this is provided by a recent study by Kotiaho *et al.* (2001) in which male courtship rate in *O. taurus* was shown to be condition-dependent. There was high genetic variance in courtship rate and females showed a strong directional mating preference for males with higher courtship rates. More importantly though, courtship rate was genetically correlated with condition and found to be unrelated to male morphology, so that a hornless sneak with a high courtship rate will not only be preferred by females but this trait should convey heritable variation in condition to her offspring (Kotiaho *et al.*, 2001). Qualitatively similar findings have been suggested for a number of bird species (Wetton & Parkin, 1991; Mulder *et al.*, 1994; Møller & Thornhill, 1998; Hoi-Leitner *et al.*, 1999; Møller, 2000).

Nevertheless, the presence of sneaks in the population may represent a significant cost for females. Copulation lasts for 2–3 min (Tomkins & Simmons, 2000) during which females are unable to continue provisioning. We found that increasing the frequency of sneaks in the population increased the total number of copulations performed by a female. Associated with this increased copulatory activity was a significant reduction in the number of brood masses produced. Females may minimize the costs of continued courtship and mating by permitting sneaks to copulate, what Thornhill & Alcock (1983) referred to as convenience polyandry. Alternatively, these costs may be outweighed by the genetic benefits accrued by mating with high condition sneak males.

Concluding remarks

Although paternal care is generally rare in insects (Zeh & Smith, 1985), those species in which it does occur represent ideal models for the experimental analysis of facultative adjustments in parental care. Paternal care has been associated with high paternity in male brooding water bugs (Smith, 1979), although it seems that high paternity in this species is fixed across breeding episodes

by the demand for repeated copulations by the caring male prior to oviposition. Male burying beetles provide extended paternal care via the preparation of carcasses and the feeding of altricial larvae (Eggert & Müller, 1997). Facultative adjustment of paternal care has been demonstrated in *Nicrophorus orbicollis* (Scott, 1998) but it is not known if males adjust their care in relation to confidence of paternity. Nutrient provisioning by male katydids may also be facultative, depending on a male's probability of fertilizing eggs (Simmons, 1995; Simmons *et al.*, 1999). As noted by Wright (1998) studies of birds have dominated this area of research, yet birds may not be the ideal models for the experimental manipulations that are required to elucidate the link between paternity and paternal care. Our study illustrates the utility of insect models in addressing the complex link between paternity and paternal care, and we hope it will stimulate an increased effort in this area of research.

Acknowledgments

References

Alexander, R.D. 1974. The evolution of social behaviour. *Ann. Rev. Ecol. Syst.* **5**: 325–383.

Alexander, R.D. & Borgia, G. 1979. On the origin and basis of the male–female phenomenon. In: *Sexual Selection and Reproductive Competition in Insects* (M. S. Blum & N. A. Blum, eds), pp. 417–440. Academic Press, New York.

Birkhead, T.R. & Møller, A.P. 1992. *Sperm Competition in Birds*. Academic Press, London.

Birkhead, T.R. & Møller, A.P. 1998. *Sperm Competition and Sexual Selection*. Academic Press, London.

Birks, S.M. 1997. Paternity in the Australian brush-turkey, *Alectura lathami*, a megapode bird with uniparental male care. *Behav. Ecol.* **8**: 560–568.

Boorman, E. & Parker, G.A. 1976. Sperm (ejaculate) competition in *Drosophila melanogaster*, and the reproductive value of females to males in relation to female age and mating status. *Ecol. Entomol.* **1**: 145–155.

Burke, T., Davies, N.B., Bruford, M.W. & Hatchwell, B.K. 1989. Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* **338**: 249–251.

Clutton-Brock, T.H. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton.

Cook, D.F. 1987. Sexual selection in dung beetles 1. A mutivariate study of the morphological variation in two species of dung beetle *Onthophagus* (Scarabaeidae: Onthophagini). *Aust. J. Zool.* **35**: 123–132.

Cook, D.F. 1988. Sexual selection in dung beetles. 2. Female fecundity as an estimate of male reproductive success in relation to horn size, and alternative behavioural strategies in *Onthophagus binodis* Thunberg (Scarabaeidae: Onthophagini). *Aust. J. Zool.* **36**: 521–532.

Cook, P.A., Harvey, I.F. & Parker, G.A. 1997. Predicting variation in sperm precedence. *Phil. Trans. Roy. Soc. Lond. B* **352**: 771–780.

Davies, N.B., Hatchwell, B.J., Robson, T. & Burke, T. 1992. Paternity and parental effort in dunnocks *Prunella modularis*: how good are male chick-feeding rules? *Anim. Behav.* **43**: 729–745.

Dixon, A., Ross, D., O'Malley, S.L.C. & Burke, T. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature* **371**: 698–700.

Dunn, P.O. & Cockburn, A. 1996. Evolution of male parental care in a bird with almost complete cuckoldry. *Evolution* **50**: 2542–2548.

Eggert, A.K. & Müller, J.K. 1997. Biparental care and social evolution in burying beetles: lessons from the larder. In: *The Evolution of Social Behaviour in Insects and Arachnids* (J. C. Choe & B. J. Crespi, eds). Cambridge University Press, Cambridge.

Emlen, D.J. 1996. Artificial selection on horn length-body size allometry in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Evolution* **50**: 1219–1230.

Emlen, D.J. 1997. Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleotera: Scarabaeidae). *Behav. Ecol. Sociobiol.* **41**: 335–341.

Emlen, D.J. & Nijhout, H.F. 1999. Hormonal control of the male horn length dimorphism in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). *J. Insect. Physiol.* **45**: 45–53.

Freeman-Gallant, C.R. 1996. Parentage and paternal care: consequences of intersexual selection in Savannah sparrows? *Behav. Ecol. Sociobiol.* **40**: 395–400.

Gowaty, P.A. 1996. Battles of the sexes and origins of monogamy. In: *Partnerships in Birds* (J. L. Black, ed.). Oxford University Press, Oxford.

Grafen, A. 1980. Opportunity cost, benefit and the degree of relatedness. *Anim. Behav.* **28**: 967–968.

Graves, J., Ortega-Ruana, J. & Slater, P.J.R. 1993. Extra-pair copulations and paternity in shags: do females choose better males? *Proc. Roy. Soc. Lond. B* **253**: 3–7.

Halffter, G. & Edmonds, W.G. 1982. *The Nesting Behaviour of Dung Beetles (Scarabaeidae): an Ecological and Evolutive Approach*. Instituto de Ecologia, Mexico.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. *J. Theor. Biol.* **7**: 1–16.

Hasselquist, D., Bensch, S. & von Schantz, T. 1995. Low frequency of extra-pair paternity in the polygynous great reed warbler, *Acrocephalus arundinaceus*. *Behav. Ecol.* **6**: 27–38.

Hatchwell, B.J. & Davies, N.B. 1990. Provisioning of nestlings by dunnocks, *Prunella modularis*, in pairs and trios: compensation reactions by males and females. *Behav. Ecol. Sociobiol.* **27**: 199–210.

Hoi-Leitner, M., Hoi, H., Romero-Pujante, M. & Valera, F. 1999. Female extra-pair behaviour and environmental quality in the serin (*Serinus serinus*): a test of the 'constrained female hypothesis'. *Proc. Roy. Soc. Lond.* **266**: 1021–1026.

Hunt, J. & Simmons, L.W. 1997. Patterns of fluctuating asymmetry in beetle horns: an experimental examination of the honest signal hypothesis. *Behav. Ecol. Sociobiol.* **41**: 109–114.

Hunt, J. & Simmons, L.W. 1998a. Patterns of parental provisioning covary with male morphology in a horned beetle (*Onthophagus taurus*) (Coleoptera: Scarabaeidae). *Behav. Ecol. Sociobiol.* **42**: 447–451.

Hunt, J. & Simmons, L.W. 1998b. Patterns of fluctuating asymmetry in beetle horns: no evidence for reliable signalling. *Behav. Ecol.* **9**: 465–470.

Hunt, J. & Simmons, L.W. 2000. Maternal and paternal effects on offspring phenotype in the dung beetle *Onthophagus taurus*. *Evolution* **54**: 936–941.

Hunt, J. & Simmons, L.W. 2001. Status-dependent selection in the dimorphic beetle *Onthophagus taurus*. *Proc. Roy. Soc. Lond. B* **268**: 2409–2414.

Hunt, J. & Simmons, L.W. 2002. Behavioural dynamics of biparental care in the dung beetle *Onthophagus taurus*. Anim. Behav., in press.

Hunt, J., Kotiaho, J.S. & Tomkins, J.L. 1999. Dung pad residence time covaries with male morphology in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). *Ecol. Entomol.* **24**: 174–180.

Kempenaers, B. & Sheldon, B.C. 1997. Studying paternity and paternal care: pitfalls and problems. *Anim. Behav.* **53**: 423–427.

Kempenaers, B., Verheyen, G.R., van de Broeck, T., Burke, T., van Broeckhoven, C. & Dhondt, A.A. 1992. Extra-pair paternity results from female preference for high quality males in the blue tit. *Nature* **357**: 494–496.

Koenig, W.D. 1990. Opportunity of parentage and nest destruction in polygynandrous acorn woodpeckers, *Melanerpes formicivorus*. *Behav. Ecol.* **1**: 55–61.

Kotiaho, J.S., Simmons, L.W. & Tomkins, J.L. 2001. Towards a resolution to the lek paradox. *Nature* **410**: 684–686.

Lee, J.M. & Peng, Y.S. 1982. Influence of manure availability and nesting density on the progeny size of *Onthophagus gazella*. *Environ. Entomol.* **11**: 38–41.

Lifjeld, J.T., Dunn, P.O., Robertson, R.J. & Boag, P.T. 1993. Extra-pair paternity in monogamous tree swallows. *Anim. Behav.* **45**: 213–229.

Lifjeld, J.T., Slagsvold, T. & Ellengren, H. 1998. Experimentally reduced paternity affects paternal effort and reproductive success in pied flycatchers. *Anim. Behav.* **55**: 319–329.

Lubjuhn, T., Curio, E., Muth, S.C., Brün, J. & Epplen, T.J. 1993. Influence of extra-pair paternity on parental care in great tits (*Parus major*). In: *DNA Fingerprinting: State of the Science* (S. D. J. Pena, R. Chakraborty, J. T. Epplen & A. J. Jeffreys, eds). Birkhäuser-Verlag, Bern.

Maynard Smith, J. 1978. *The Evolution of Sex*. Cambridge University Press, Cambridge.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

Moczek, A.P. 1999. Facultative paternal investment in the polyphenic beetle *Onthophagus taurus:* the role of male morphology and social context. *Behav. Ecol.* **10**: 641–647.

Moczek, A.P. & Emlen, D.J. 2000. Male horn dimorphisms in the scarab beetle, *Onthophagus taurus:* do alternative reproductive tactics favor alternative phenotypes. *Anim. Behav.* **59**: 459–466.

Møller, A.P. 1988. Paternity and parental care in the swallow, *Hirundo rustica*. *Anim. Behav.* **36**: 996–1005.

Møller, A.P. 1991. Defence of offspring by male swallows, *Hirundo rustica*, in relation to participation in extra-pair copulations by their mates. *Anim. Behav.* **42**: 261–267.

Møller, A.P. 2000. Male parental care, female reproductive success, and extrapair paternity. *Behav. Ecol.* **11**: 161–168.

Møller, A.P. & Birkhead, T.R. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. *Behaviour* **118**: 170–186.

Møller, A.P. & Birkhead, T.R. 1993. Certainty of paternity covaries with parental care. *Behav. Ecol. Sociobiol.* **33**: 261–268.

Møller, A.P. & Cuervo, J.J. 2000. The evolution of paternity and paternal care in birds. *Behav. Ecol.* **11**: 472–485.

Møller, A.P. & Thornhill, R. 1998. Male parental care, differential parental investment and sexual selection. *Anim. Behav.* **55**: 1507–1515.

Morton, E.S., Forman, L. & Braun, M. 1990. Extra-pair fertilizations and the evolution of colonial breeding in purple martins. *Auk* **107**: 275–283.

Mulder, R.A., Dunn, P.O., Cockburn, A., Lazenby-Cohen, K.A. & Howell, M.J. 1994. Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proc. Roy. Soc. Lond. B* **255**: 223–229.

Norris, K.J. 1990. Female choice and the evolution of the conspicuous plumage coloration of monogamous male great tits. *Behav. Ecol. Sociobiol.* **26**: 129–138.

Parker, G.A. 1990. Sperm competition games: sneaks and extrapair copulations. *Proc. Roy. Soc. Lond. B* **242**: 127–133.

Ridley, M. 1978. Paternal care. *Anim. Behav.* **26**: 904–932.

Schwagmeyer, P.L. & Mock, D.W. 1993. Shaken confidence of paternity. *Anim. Behav.* **46**: 1020–1022.

Schwagmeyer, P.L., St. Clair, R.C., Moodie, J.D., Lamey, T.C., Schnell, G.D. & Moodie, M.N. 1999. Species differences in male parental care in birds: a reexamination of correlates with paternity. *Auk* **116**: 487–503.

Scott, M.P. 1998. Facultative adjustment of the duration of parental care by burying beetles. *J. Insect. Behav.* **11**: 597–603.

Sheldon, B.C. & Ellegren, H. 1998. Paternal effort related to experimentally manipulated paternity of male collared flycatchers. *Proc. Roy. Soc. Lond. B* **265**: 1737–1742.

Simmons, L.W. 1995. Male bushcrickets tailor spermatophores in relation to their remating interval. *Funct. Ecol.* **9**: 881–886.

Simmons, L.W., Beesley, L., Lindhjem, P., Newbound, D., Norris, J. & Wayne, A. 1999. Nuptial feeding by male bushcrickets: an indicator of male quality? *Behav. Ecol.* **10**: 263–269.

Smith, R.L. 1979. Repeated copulation and sperm precedence: paternity assurance for a male brooding water bug. *Science* **205**: 1029–1031.

Smith, R.L. 1984. *Sperm Competition and the Evolution of Animal Mating Systems*. Academic Press, Orlando.

Smith, S.M. 1988. Extra-pair copulations in black capped chickadees: the role of the female. *Behaviour* **107**: 15–23.

Sowig, P. 1996. Duration and benefits of biparental brood care in the dung beetle *Onthophagus vacca* (Coleoptera: Scarabaeidae). *Ecol. Entomol.* **21**: 81–86.

Stutchbury, B.J., Rhymer, J.M. & Morton, E.S. 1994. Extrapair paternity in hooded warblers. *Behav. Ecol.* **5**: 384–392.

Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge.

Tomkins, J.L. & Simmons, L.W. 2000. Sperm competition games played by dimorphic male beetles: fertilisation gains with equal mating access. *Proc. Roy. Soc. Lond. B* **267**: 1547–1553.

Trivers, R.L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (B. Campbell, ed.). Aldine Press, Chicago, IL.

Weatherhead, P.J., Montgomerie, R., Gibbs, H.L. & Boag, P.T. 1994. The cost of extra-pair fertilizations to female red-winged blackbirds. *Proc. Roy. Soc. Lond. B* **258**: 315–320.

Werren, J.H., Gross, M.R. & Shine, R. 1980. Paternity and the evolution of male parental care. *J. Theor. Biol.* **82**: 619–631.

Westneat, D.F. 1988. Male parental care and extrapair copulations in the indigo bunting. *Auk* **105**: 149–160.

Westneat, D.F. 1995. Paternity and paternal behaviour in the red-winged blackbird, *Agelais phoeniceus. Anim. Behav.* **49**: 21–35.

Westneat, D.F. & Sherman, P. 1993. Parentage and the evolution of parental behaviour. *Behav. Ecol.* **4**: 66–77.

Westneat, D.F., Clarke, A.B. & Rambo, K.C. 1995. Within-brood patterns of paternity and paternal behaviour in red-winged blackbirds. *Behav. Ecol. Sociobiol.* **37**: 349–356.

Wetton, J.H. & Parkin, D.T. 1991. An association between fertility and cuckoldry in the house sparrow, *Passer domesticus. Proc. Roy. Soc. Lond. B* **245**: 227–233.

Whittingham, L.A. & Lifjeld, J.T. 1995. High paternal investment in unrelated young: extra-pair paternity and male parental care in house martins. *Behav. Ecol. Sociobiol.* **37**: 103–108.

Whittingham, L.A., Taylor, P.D. & Robertson, R.J. 1992. Confidence of paternity and male parental care. *Am. Nat.* **139**: 1115–1125.

Winkler, D.W. 1987. A general model for parental care. *Am. Nat* **130**: 526–543.

Wright, J. 1998. Paternity and paternal care. In: *Sperm Competition and Sexual Selection* (T. R. Birkhead & A. P. Møller, eds). Academic Press, London.

Wright, J. & Cotton, P.A. 1994. Experimentally induced sex differences in parental care: an effect of certainty of paternity? *Anim. Behav.* **47**: 1311–1322.

Xia, X. 1992. Uncertainty of paternity can select against paternal care. *Am. Nat.* **139**: 1126–1129.

Yezerinac, S.M., Weatherhead, P.J. & Boag, P.T. 1996. Cuckoldry and lack of parentage-dependent paternal care in yellow warblers: a cost-benefit approach. *Anim. Behav.* **52**: 821–832.

Zeh, D.W. & Smith, R.L. 1985. Parental investment by terrestrial arthropods. *Am. Zool.* **25**: 785–805.