



# Behavioural dynamics of biparental care in the dung beetle *Onthophagus taurus*

JOHN HUNT & LEIGH W. SIMMONS

Evolutionary Biology Research Group, Department of Zoology, University of Western Australia

(Received 14 September 2001; initial acceptance 17 October 2001;  
final acceptance 2 January 2002; MS. number: 7063)

In the dimorphic dung beetle *Onthophagus taurus* major males provide assistance during offspring provisioning. We examined the behavioural dynamics of biparental care to quantify directly how males and females allocate time to parental and nonparental behaviours and to determine whether parents adjust their level of investment relative to their partner's contribution. Females allocated more of their time budget to parental behaviours than males. The proportion of time females allocated to parental behaviours increased after oviposition while that of a male decreased. Male paternity assurance behaviours were negatively associated with male and female parental behaviours. Theoretical models predict that the investment provided by the members of a cooperative pair should be negatively correlated and that any shortfall of one parent should be partially compensated for by the other. In the absence of a male, unassisted females allocated more time to parental care, and performed more parental behaviours. However, compensation was incomplete as unassisted females performed fewer parental behaviours than pairs, resulting in significantly lighter brood masses (the egg and its associated dung supply). Males performed more parental behaviours when paired with small females, and small females more than large females. Contrary to prediction, the investments provided by males and females in a cooperative pair were positively correlated. Males coordinated their parental behaviours with the females rather than acting independently. Since parental behaviours were directly related to the weight of brood masses, the observed parental interactions will have important fitness consequences in this species.

© 2002 The Association for the Study of Animal Behaviour. Published by Elsevier Science Ltd. All rights reserved.

Strategies of parental care often differ considerably across mating systems (Clutton-Brock 1991). In uniparental systems, carers are expected to invest according to the optimal trade-off between the benefits of current investment to offspring fitness and the costs of this investment to future reproduction (Williams 1966). However, in systems with biparental care an individual's optimal investment will depend not only on this trade-off but also on the amount of investment provided by the cooperating partner (Williams 1966; Trivers 1972). Since members of a cooperative pair may not share a common goal of maximizing their joint fitness (Trivers 1972), sexual conflict over the amount and division of care will exist whenever the investment optima of the sexes differ. As a result, the optimal investment of two parents is likely to reflect the outcome of a contest played between the sexes over behavioural or evolutionary time (Westneat & Sargent 1996).

Correspondence and present address: J. Hunt, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney 2052, Australia (email: [john.hunt@unsw.edu.au](mailto:john.hunt@unsw.edu.au)). L. W. Simmons is at the Department of Zoology, University of Western Australia, Nedlands, WA 6907, Australia.

A number of theoretical models have attempted to predict how the investment patterns of one parent should change relative to its partner's investment (Chase 1980; Houston & Davies 1985; Winkler 1987; Lazarus 1989). Under most conditions, the parental investments of two cooperating individuals are expected to be negatively correlated, with the shortfall of one partner being compensated for by the other (Chase 1980; Houston & Davies 1985; Winkler 1987). However, the extent of this compensatory response will depend upon the slopes of the reaction curves for the sexes (the curve of optimal male investment plotted on female investment and vice versa) and their point of intersection (Chase 1980; Winkler 1987). If the reaction curves intersect and the slope of each curve is less than  $-1$ , the intersection point should represent an evolutionarily stable strategy (ESS) for both parents and each parent should respond to a reduction in its partner's care by partially increasing its own investment (Chase 1980). Subsequent alternating investments by each parent will represent a bargaining process mediated through a sequence of smaller and smaller changes in investment until the ESS is reached (Chase 1980). However, if the reaction curves do not intersect or the

slopes of the curves are greater than  $-1$ , other evolutionary outcomes are conceivable (Chase 1980; Winkler 1987). For example, if the female's curve is above that of the male and they do not intersect, the male should desert and the female ESS would be to take over complete care of the offspring. The reverse should be true if the male curve exceeds the female curve (Chase 1980). If the reaction curves have a slope greater than  $-1$  at the region of intersection, the resulting intersection point will be unstable and if one parent reduces its investment, the other should respond by increasing its own investment by a level that more than compensates for this reduction (Chase 1980). Subsequent adjustments by parents will continue to increase until one parent becomes responsible for all investment.

Empirical evidence for compensatory responses of parents to changes in the level of investment provided by their partner has come almost exclusively from studies on biparental birds, and these have yielded conflicting results. In the majority of bird species, a combination of partner removal (e.g. Alatalo et al. 1982; Leffelaar & Robertson 1986; Lyon et al. 1987; Wolf et al. 1988; Bart & Tornes 1989; Dunn & Hannon 1989; Whillans & Falls 1990; Dunn & Robertson 1992; Markman et al. 1996) and handicapping techniques (e.g. Leffelaar & Robertson 1986; Wright & Cuthill 1989, 1990a; Markman et al. 1995) have shown that parents provide only partial compensation for their partner's reduction. In other species, however, parents are able to compensate fully for this reduction (e.g. Weatherhead 1979; Smith et al. 1982; Greenlaw & Post 1985; Wolf et al. 1990; Wright & Cuthill 1990b; Saino & Møller 1995) or show no compensatory response (e.g. Muldal et al. 1986; Lozano & Lemon 1996). Recently, Møller (2000) provided comparative evidence suggesting that the observed variation in the compensatory responses of parents in partner removal studies is, in part, related to the relative importance of the partner's contribution. That is, in species where a partner contributes relatively little to investment, a parent should be able to compensate fully for this loss or it may not even be necessary to compensate at all (Bart & Tornes 1989; Slagsvold & Lifjeld 1990; Møller 2000). Such a relationship may also explain why ecological conditions often have a pronounced effect on the compensatory responses of parents within species (Lyon et al. 1987; Dunn & Robertson 1992).

The biparental care of eggs or young is typically uncommon amongst invertebrates but does occur in species where competition for a larval resource is intense, or when parents must lay down provisions for or directly feed their young (Zeh & Smith 1985; Clutton-Brock 1991). However, in dung beetles belonging to the genus *Onthophagus*, biparental care appears common (Lee & Peng 1982; Cook 1988; Sowig 1996; Hunt & Simmons 1998a, 2000; Moczek 1999). During reproduction, members of this genus remove portions of dung from the pad and pack it into the blind end of tunnels constructed beneath the dung pad (Halffter & Edmonds 1982). A single egg is then deposited into an egg chamber and sealed; one egg and its associated dung provision constitutes a brood mass (Halffter & Edmonds 1982).

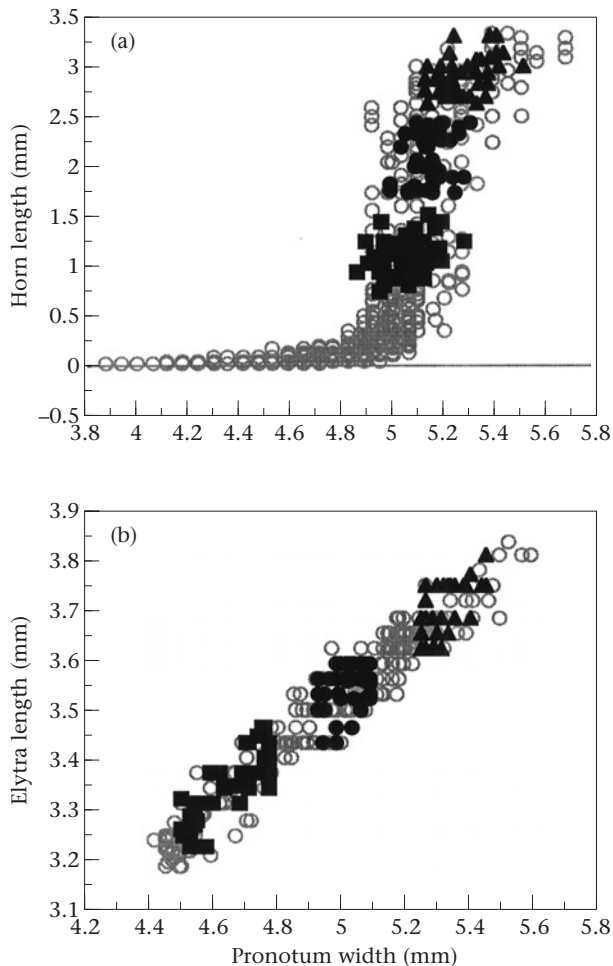
In many onthophagine dung beetles males are dimorphic: large 'major' males develop enlarged horns on the head and/or pronotum while small 'minor' males remain hornless (Cook 1987; Emlen 1996; Hunt & Simmons 1998b). Studies examining the role of males during provisioning have shown that it is generally only the major male that provides assistance during the production of a brood mass (Cook 1988; Hunt & Simmons 1998a, 2000; Moczek 1999). In *O. taurus*, all horned males provide a fixed level of care when paired with females of average size, irrespective of their own body size. Male care results in the production of significantly heavier brood masses than those produced by females provisioning without assistance (Hunt & Simmons 2000). In contrast, the amount of care that is provided by an unassisted female is largely determined by her body size, with larger females producing significantly heavier brood masses (Hunt & Simmons 2000). However, we have no information regarding behavioural interactions between the sexes during provisioning or whether males and females adjust their behaviour according to their partner's investment. Since offspring size is determined largely by the quantity of dung provided in the brood mass (Hunt & Simmons 1997), the outcome of parental interactions will have a pronounced effect on the phenotype (Hunt & Simmons 2000) and future adult fitness of offspring (Hunt & Simmons 2001).

Traditionally, empirical studies examining compensatory responses of parents have used either partner removal experiments or handicapping techniques to manipulate the amount of investment provided by one partner. A potential criticism of partner removal studies is that the compensatory responses of parents may be different from those when a partner's investment is reduced rather than removed, especially if the outcome of care giving is determined by a 'bargaining process' as envisaged by Chase (1980). As a result, it is often more informative to compare the compensatory responses of parents in partner removal studies with variation in compensatory responses of parents arising from natural variation in relative investment within cooperative pairs. We used both male removal experiments and variation in natural levels of investment provided by parents of differing sizes to quantify directly how time is allocated to parental and nonparental behaviours between the sexes and to determine whether parents adjust their level of investment relative to their partner's contribution.

## METHODS

### General Procedures

We collected *O. taurus* with baited pitfall traps from Margaret River in the southwest of Western Australia, where this species is extremely common. Beetles were maintained for 2 weeks in a mixed laboratory culture and provided with constant access to fresh dung to ensure they were reproductively mature and mated. Five 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



**Figure 1.** The three (a) male and (b) female size classes selected from a natural population ( $\circ$ ) for the breeding and behavioural experiments.  $\blacktriangle$ : Large;  $\bullet$ : medium;  $\blacksquare$ : small.

250 ml of cow dung, and maintained for 1 week at 25°C and a 14:10 h light:dark regime. We then sieved the breeding chambers and removed brood masses. We buried brood masses in moist sand and reared them to adulthood. On emergence, the offspring were maintained in single-sex populations for 2 weeks and provided with constant access to fresh dung. Before the experiments, we measured the pronotum widths of males and females, with digital callipers, and the horn lengths of males and the elytra length of females, with an eyepiece graticule in a binocular microscope. The beetles were frozen after the experiments.

## Experimental Procedure

### Breeding experiment

To examine the amount of investment provided to offspring when the body size of parents differed, we separated both major males and females into three discrete size classes across their natural size range (Fig. 1a, b). Males and females in each size category were randomly paired in a  $3 \times 3$  design based on these size classes, with 15 replicate pairs in each treatment. Pairs were estab-

lished in individual breeding chambers three-quarters filled with moist sand and 250 ml of cow dung, and maintained for 2 weeks at 25°C and a 14:10 h light:dark regime. We then sieved the breeding chambers and removed brood masses. We used a dissecting probe to remove excess sand from the brood masses and dried them to a 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.

### Behavioural analysis of parental care

To determine the proximate mechanisms of compensatory adjustments in the levels of investment provided by parents, we examined the provisioning behaviours of the sexes, with the same  $3 \times 3$  design. We examined three replicate pairs per treatment ( $N=27$  pairs). In addition, we recorded three replicate females in each of the female size classes ( $N=9$  females) provisioning without male assistance. These females were mated with a randomly selected major male prior to recording.

We used glass ant farms to examine the provisioning behaviours of parents. We constructed ant farms from two sheets of 0.5-mm glass ( $215 \times 130$  mm) separated by two glass strips ( $200 \times 15$  mm) along their length and a single strip along their width ( $130 \times 15$  mm). We used a single strip ( $130 \times 15$  mm) to seal the entrance once parents had been added. The ant farms were held together with four alligator clips along their length and were mounted in wooden bases to provide stability. This design created an internal sealed chamber with dimensions of  $200 \times 100$  mm for observation.

Each ant farm was three-quarters filled with moist sand and topped with 50 ml of fresh cow dung. We added the female from each pair to an independent chamber. Once a breeding tunnel had been constructed and the female had started provisioning a brood mass, we introduced her mate into the tunnel and once paternal assistance was observed, we recorded the behaviours of the pair. We recorded the behaviours of unassisted females when the first portion of dung had been packed into the brood chamber. We used a time lag video recorder (Sony SVT-124P) 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 pair was recorded for the entire duration required to provision a single brood mass successfully. As this may take up to 14 h, all recordings were made at a tape speed of 10 frames/s. At the completion of recording, we removed the brood mass from the observation chamber, dried it to a constant weight at 60°C, removed, excess sand, with a dissecting probe, and weighed it to the nearest 0.01 g.

The behaviours of parents during offspring provisioning can be broadly categorized as either parental or nonparental. Behaviours were collectively described as parental if they directly contributed to the production of the brood mass: (1) Removing dung from pad: a small portion of dung was separated from the pad; (2) Removing dung from tunnel: a small portion of dung was collected from the tunnel where it had been stored; (3) Carrying: the portion of dung was carried to the brood

chamber; (4) Packing: the dung was packed into the blind end of the brood chamber; and (5) Returning: the parent returned from the brood chamber to either the pad or tunnel to collect more dung. In contrast, nonparental behaviours do not benefit the offspring. In males, these behaviours predominantly represent paternity assurance behaviours (Hunt & Simmons, *in press*) and included: (1) Patrolling: the male moved up and down the tunnel without collecting or carrying portions of dung; (2) Guarding: the male remained motionless at the entrance to the breeding tunnel or brood chamber; and (3) Interacting with female: which included head-to-head interactions with the female, courtship and mating. In paired females, nonparental behaviours included (1) Interacting with the male (as defined for males) and (2) Grooming: the female groomed her head and eyes with her forelegs. In unassisted females, the only nonparental behaviour was grooming.

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

### Statistical Analysis

All analyses were performed on the proportion of time spent providing care and the number of caring behaviours required to produce a single brood mass. Proportional data were arcsine square-root transformed to account for their characteristic non-normal distributions (Zar 1985) but for ease of interpretation results are presented as untransformed percentages. The number of caring behaviours performed were log transformed to meet the assumptions of a normal distribution and heterogeneity of variances amongst treatments (Zar 1985). Means are given with SEs and statistical tests are two tailed.

## RESULTS

### Breeding Experiment

To examine the weight and number of brood masses produced by breeding pairs that differed in size, we used a two-factor ANOVA, with parental size classes as the main effects and brood mass weight and number as the dependent variables. Pairs failing to produce any brood masses were excluded from the analysis so that sample sizes for each treatment varied (see Table 1). There was no effect of male ( $F_{2,94}=1.39$ ,  $P=0.25$ ) or female size class ( $F_{2,94}=1.62$ ,  $P=0.21$ ) on the weight of brood masses produced by pairs and there was no significant interaction ( $F_{4,94}=1.01$ ,  $P=0.41$ ; Table 1). Similarly, there was no effect of parental size on the number of brood masses produced by a breeding pair (male:  $F_{2,94}=0.39$ ,  $P=0.68$ ; female:  $F_{2,94}=0.20$ ,  $P=0.82$ ; male  $\times$  female:  $F_{4,94}=0.70$ ,  $P=0.59$ ; Table 1).

### Sex Differences in Parental Behaviours

On average, females in a cooperative pair spent proportionately more time performing caring behaviours than

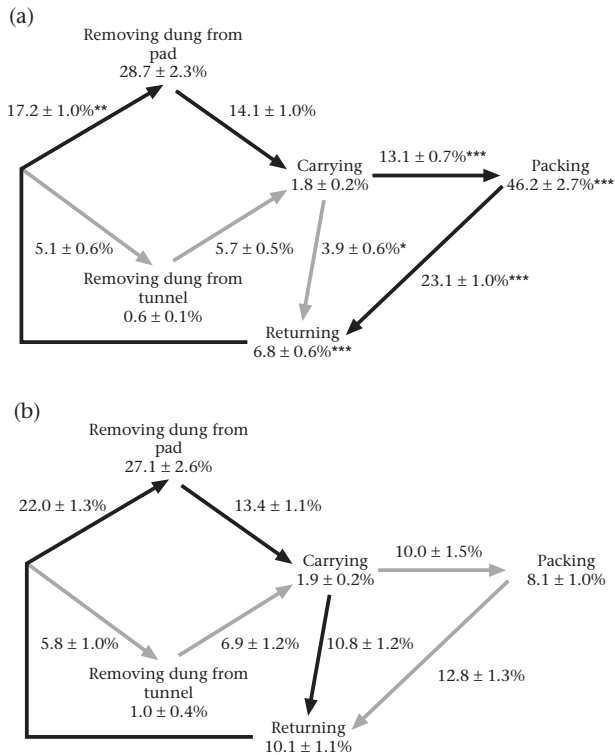
**Table 1.** The mean weight and number  $\pm$  SE of brood masses (the egg and associated dung) produced by pairs in each of the nine parental size classes

Male size	Female size	Brood mass weight (g)	Brood mass number	N
Small	Small	1.57 $\pm$ 0.03	23.67 $\pm$ 1.40	12
	Medium	1.60 $\pm$ 0.02	23.50 $\pm$ 0.90	10
	Large	1.54 $\pm$ 0.05	24.77 $\pm$ 1.06	13
Medium	Small	1.58 $\pm$ 0.04	23.23 $\pm$ 1.06	13
	Medium	1.57 $\pm$ 0.03	25.33 $\pm$ 1.00	9
	Large	1.64 $\pm$ 0.03	23.33 $\pm$ 0.93	12
Large	Small	1.55 $\pm$ 0.03	23.39 $\pm$ 1.26	13
	Medium	1.62 $\pm$ 0.04	22.50 $\pm$ 1.67	8
	Large	1.58 $\pm$ 0.02	23.85 $\pm$ 0.95	13

males (females: 84.1  $\pm$  1.9%; males: 48.2  $\pm$  2.6%; paired  $t$  test:  $t_{26}=18.69$ ,  $P=0.0001$ ). The most common behavioural sequence of a paired female was to remove dung from the pad, carry it to the brood chamber, pack it into the brood mass and return to the pad to collect more dung (Fig. 2a). In contrast, a caring male was more likely to pass the dung portion to the female already inside the brood chamber and return to the pad to collect more dung, rather than packing this dung portion himself (Fig. 2b). As a result, females spent proportionately more time than males packing dung into the brood chamber and less time returning to the pad to gather more dung (Fig. 2a, b).

To see whether parental and nonparental behaviours varied over time, we separated our data into six 30-min time intervals and calculated time budgets for each interval. These time intervals were standardized to the time when the female deposited the egg in the brood mass and represented three intervals before ( $-90$ ,  $-60$  and  $-30$  min) and three after oviposition (30, 60 and 90 min). A repeated measures ANOVA showed that the proportion of time females spent on all parental behaviours increased over time ( $F_{5,130}=8.30$ ,  $P=0.0001$ ; Fig. 3a). Univariate tests on the individual parental behaviours revealed that there was a significant increase in the proportion of time spent packing dung into the brood chamber once the egg had been deposited ( $F_{5,130}=87.99$ ,  $P=0.0001$ ), whereas all other parental behaviours, with the exception of removing dung from the tunnel ( $F_{5,130}=1.45$ ,  $P=0.09$ ), decreased significantly with time (Removing dung from pad:  $F_{5,130}=52.96$ ,  $P=0.0001$ ; Carrying:  $F_{5,130}=11.69$ ,  $P=0.0001$ ; Returning:  $F_{5,130}=26.84$ ,  $P=0.0001$ ; Fig. 3a). All significant univariate tests remained significant after Bonferroni adjustment.

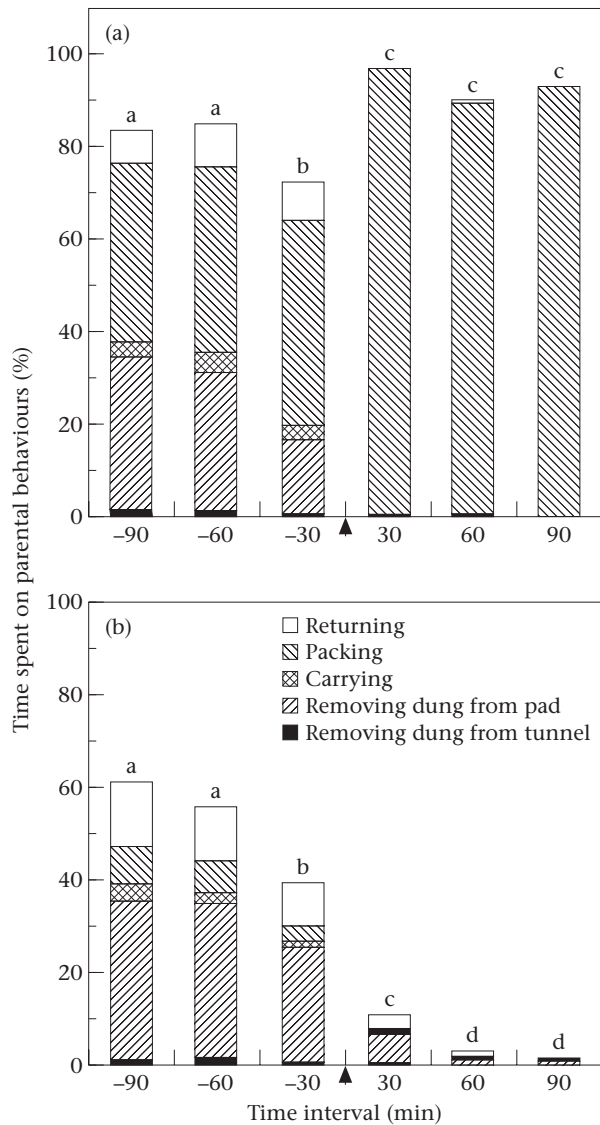
In contrast to females, the summed proportion of time a male spent providing all parental behaviours decreased over time ( $F_{5,130}=58.28$ ,  $P=0.0001$ ; Fig. 3b). Univariate tests revealed that this decrease was significant for all male parental behaviours except removing from tunnel (Removing dung from tunnel:  $F_{5,130}=2.00$ ,  $P=0.06$ ; Removing dung from pad:  $F_{5,130}=27.90$ ,  $P=0.0001$ ; Carrying:  $F_{5,130}=11.54$ ,  $P=0.0001$ ; Packing:  $F_{5,130}=11.44$ ,  $P=0.0001$ ; Returning:  $F_{5,130}=22.74$ ;  $P=0.0001$ ; Fig. 3b).



**Figure 2.** Ethograms showing the parental behaviour pathways taken by (a) females and (b) males during offspring provisioning. For both males and females, the most frequently taken behavioural pathways are represented by dark arrows. The values presented under each parental behaviour represent the mean  $\pm$  SE percentage of time spent on that behaviour. The values associated with arrows represent the mean percentage  $\pm$  SE, out of all possible behavioural transitions, that one parental behaviour was followed by another. Since each parental behaviour could be preceded by a nonparental behaviour, these percentages do not add to 100%. To compare the proportion of time spent on each parental behaviour and the transitions between each parental behaviour between males and females, we used paired *t* tests. Significant differences between the sexes are presented in (a): \* $P < 0.01$ , \*\* $P < 0.001$ , \*\*\* $P < 0.0001$ . All differences remained significant after Bonferroni adjustment.

The decrease in male parental behaviours with time was associated with an increase in the proportion of time spent on nonparental, paternity assurance behaviours ( $F_{5,130} = 56.44$ ,  $P = 0.0001$ ; Fig. 4). Univariate tests revealed that the proportion of time spent interacting with females was lower after oviposition ( $F_{5,130} = 6.48$ ,  $P = 0.0001$ ), while the proportion of time spent mate guarding was higher after oviposition ( $F_{5,130} = 82.01$ ,  $P = 0.0001$ ; Fig. 4). While the proportion of time spent patrolling the breeding tunnel tended to be lower after oviposition, this was not significant after Bonferroni adjustment ( $F_{5,130} = 3.12$ ;  $P = 0.011$ ; Fig. 4). All other significant univariate tests remained significant after Bonferroni adjustment.

On all occasions, the male began courting the female immediately when introduced into the breeding tunnel. This resulted in an initial mating within 10 min of introduction, prior to the onset of recordings. However, in 15 out of 27 pairs (56%), males mated again during the

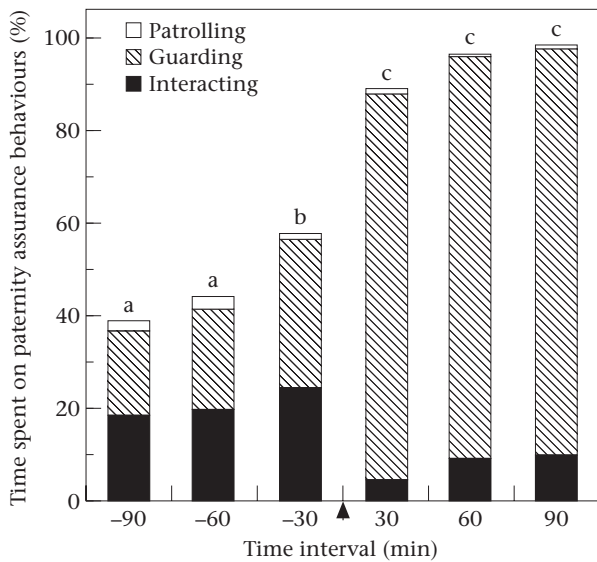


**Figure 3.** The proportion of time that (a) females and (b) males spent on each of the parental behaviours across each of six time intervals before and after oviposition. For both males and females, significant differences in the summed proportion of time spent providing parental behaviours between the time intervals were determined with a Fisher's PLSD post hoc test from the repeated measures ANOVA. Different letters represent significant differences at the  $P < 0.05$  level. The arrowhead represents the time at which oviposition occurred.

provisioning of a brood mass. The occurrence of second matings was nonrandomly distributed across time intervals ( $\chi^2_5 = 39.80$ ,  $P = 0.0001$ ), with 11 matings (73%) occurring in the time interval immediately prior to oviposition and the remaining four (27%) between 60 and 30 min prior to oviposition.

### Compensatory Responses of Unassisted Females

To see whether unassisted females had a higher investment to compensate for the lack of a partner, we used a two-factor ANOVA with female size class and presence or



**Figure 4.** The proportion of time that males spent on each of the paternity assurance behaviours across each of six time intervals before and after oviposition. Significant differences in the summed proportion of time spent providing parental behaviours between the time intervals were determined with a Fisher's PLSD post hoc test from the repeated measures ANOVA (see text for details). Different letters represent significant differences at the  $P < 0.05$  level. The arrowhead represents the time at which oviposition occurred.

absence of a mate as the main effects and the proportion of time females spent in all parental behaviours as the dependent variable. Females spent significantly more time providing care in the absence of a male partner ( $F_{1,30} = 66.31$ ,  $P = 0.0001$ ; unassisted females:  $99.7 \pm 0.2\%$ ; paired females:  $84.1 \pm 1.9\%$ ) but size of the female had no effect ( $F_{2,30} = 0.21$ ,  $P = 0.81$ ) nor was there a significant interaction ( $F_{2,30} = 0.28$ ,  $P = 0.76$ ). We obtained qualitatively similar results when we used the total number of caring behaviours of a female (male presence:  $F_{1,30} = 17.55$ ,  $P = 0.0002$ ; female size:  $F_{2,30} = 2.35$ ,  $P = 0.11$ ; male presence  $\times$  female size:  $F_{2,30} = 1.66$ ,  $P = 0.21$ ).

To examine the extent of compensation by unassisted females, we compared the total number of parental behaviours of unassisted females with the combined total number of both parents within a cooperative pair. Despite the increased level of care provided by unassisted females, this compensation was incomplete because the total number of caring behaviours of unassisted females was significantly lower than for pairs ( $F_{1,35} = 11.08$ ,  $P = 0.0022$ ; unassisted females:  $326.44 \pm 33.38$  caring behaviours; pairs:  $378.48 \pm 25.69$  caring behaviours), resulting in the production of significantly lighter brood masses ( $F_{1,35} = 4.95$ ,  $P = 0.03$ ; unassisted females:  $1.26 \pm 0.05$  g; pairs:  $1.42 \pm 0.04$  g).

### Relative Contributions of the Sexes

To see whether males or females respond to the amount of investment provided by their partner, we used a two-factor ANOVA, with male and female size classes as the main effects and the level of investment provided by the

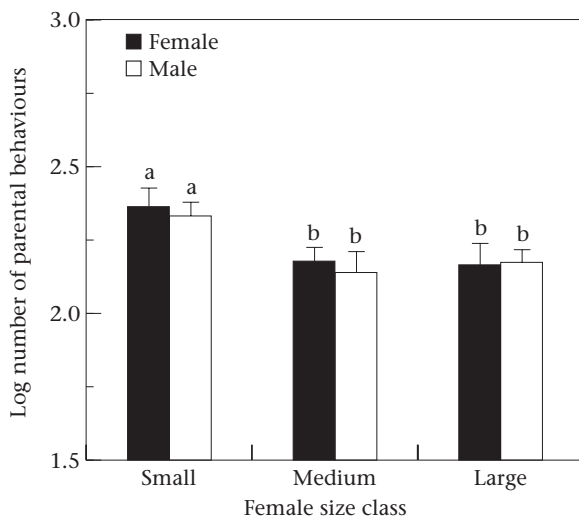
corresponding parent as the dependent variable. There was no effect of paternal size on the amount of investment of males and females (Table 2). However, there was a significant effect of female size on the number of caring behaviours of both sexes (Table 2). This occurred because males of all size classes performed more parental behaviours when paired with a small female, and because small females, irrespective of their partner's size, performed more parental behaviours than larger females (Fig. 5). Across parental size classes, the relationships between the proportion of time spent in parental behaviours by males relative to females and the number of parental behaviours of males relative to females were positive and significant (proportion:  $r_{26} = 0.658$ ,  $P < 0.01$ ; frequency:  $r_{26} = 0.387$ ,  $P = 0.033$ ; Fig. 6). Consistent with the breeding experiment, the weight of brood masses produced by pairs was not significantly influenced by male size ( $F_{2,18} = 2.57$ ,  $P = 0.10$ ) or female size ( $F_{2,18} = 0.42$ ,  $P = 0.66$ ) and there was no significant interaction ( $F_{4,18} = 1.66$ ,  $P = 0.20$ ).

To ascertain the behavioural mechanisms generating the positive covariation between maternal and paternal care, we analysed our data in two ways. First, to examine the sequential distribution of the remove dung from pad behaviour between the sexes for the entire duration required to produce a brood mass, we used a serial runs test for nominal scale categories (Zar 1985). We used the remove dung from pad behaviour because it showed the strongest positive relationship between males and females in a cooperative pair ( $r_{26} = 0.62$ ,  $P = 0.0001$ ). This procedure yields an ordered sequence of events between the sexes that can be tested against the null hypothesis of randomness (Zar 1985). If the male and female in a cooperating pair are acting independently, the sequential distribution of this caring behaviour should be random. We calculated the sequential distribution of this behaviour for each of the 27 pairs and then used a Fisher's combined probability across pairs to test for overall significance. The combined probability showed that the sequential distribution of this caring behaviour between the sexes differed significantly from a random distribution ( $\chi^2_{26} = 87.19$ ,  $P = 0.003$ ).

Second, as the above analysis does not incorporate the time intervals between the sequential behaviours of the sexes, we analysed our data quantitatively in two further ways. First, we examined the time taken for each parent to respond (with its own parental behaviour) to the parental behaviour of its partner. We examined the remove dung from pad behaviour and calculated the mean response time of the sexes for the entire duration required to provision a brood mass. If there is a stable temporal relationship between the provisioning behaviours of the sexes, the response time of the sexes should be nonrandomly distributed. The time taken for a male to respond to the parental behaviour of his female partner differed significantly from a random distribution (Poisson distribution:  $\chi^2_2 = 18.57$ ,  $P = 0.0001$ ), while the time taken for a female to respond to a male did not ( $\chi^2_2 = 2.06$ ,  $P = 0.36$ ). This suggests that males respond to the parental behaviour of females within a constant and restricted time window but that a female's response is independent of the male's behaviour. In addition, we examined the

**Table 2.** The results of two-factor ANOVAs for male and female sizes on the proportion of time spent in parental behaviours and the number of parental behaviours of males and females

	Proportion			Number			
	Mean square	F	P	Mean square	F	P	df
<b>Male care</b>							
Male size	$1.83 \times 10^{-2}$	0.83	0.45	$5.90 \times 10^{-2}$	2.05	0.16	2
Female size	$1.54 \times 10^{-3}$	0.07	0.93	$1.16 \times 10^{-1}$	3.99	0.04	2
Male×Female	$1.14 \times 10^{-2}$	0.52	0.72	$2.12 \times 10^{-2}$	0.73	0.58	4
Error	$2.20 \times 10^{-2}$			$2.90 \times 10^{-2}$			18
<b>Female care</b>							
Male size	$7.75 \times 10^{-3}$	0.31	0.74	$8.73 \times 10^{-2}$	3.02	0.08	2
Female size	$3.00 \times 10^{-2}$	1.20	0.32	$1.09 \times 10^{-1}$	3.76	0.04	2
Male×Female	$6.25 \times 10^{-3}$	0.25	0.91	$2.57 \times 10^{-2}$	0.89	0.49	4
Error	$2.50 \times 10^{-2}$			$2.89 \times 10^{-2}$			18

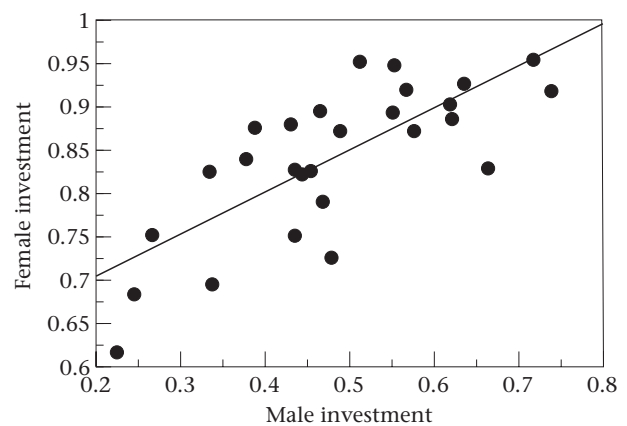
**Figure 5.** The log number of parental behaviours of males and females for each of three female size classes. Differences between treatments were determined with a Tukey test for multiple comparisons. Different letters represent significant differences at the  $P < 0.05$  level.

mean response interval of the sexes within a cooperative pair. If the parental behaviour of males is coordinated with that of females, the mean interval between parental behaviours for males and females should be positively correlated and this is what we found ( $r_{26} = 0.59$ ,  $P = 0.001$ ).

## DISCUSSION

### Division of Labour Between the Sexes

We have shown a clear division of labour between the sexes in the biparentally caring dung beetle *O. taurus*. During the provisioning of a brood mass, females allocated ca. 84%, and males only 48%, of their time budget towards parental care duties. This contrasts with a number of bird species where the male's contribution to offspring feeding either equals (e.g. Mumme & De Queiroz 1985; Leffelaar & Robertson 1986; Alatalo et al. 1988; Smith et al. 1988; Wright & Cuthill 1990a; Saino &

**Figure 6.** The proportion of time a male spent providing parental behaviours relative to the contribution of his partner.

Møller 1995) or exceeds that of the female (e.g. Holstein 1942; Alatalo et al. 1982; Kemp 1988; Dunn & Hannon 1989; Sasvãri 1990). Furthermore, while both parents were able to perform all caring behaviours, each sex had specific parental roles. A male's primary role was to remove dung from the pad and deliver it to the female in the brood chamber, while the female's primary role was to incorporate this dung into the brood mass.

Sex-specific parental roles have been shown in a number of bird species and appear to facilitate the efficiency with which biparental care is provided to offspring (e.g. Bédard & Meunier 1983; Mumme & de Queiroz 1985; Goldstein & Yom-Tov 1988; Dunn & Hannon 1989; Quinn 1990; Møller 1991; Markman et al. 1995, 1996). The presence and magnitude of sex-specific roles and the ability of each parent to perform the roles of its partner successfully is likely to be of major importance in determining the extent of compensatory responses by parents. To compensate for a partner's reduction, a parent must be able to compensate not only for the amount of lost care but also for the type of care that is provided by its partner. This will be particularly true if certain provisioning behaviours can be provided by only one sex. In *O. taurus*, the prevalence of females packing dung into the brood chamber, particularly immediately prior to

and after oviposition, undoubtedly reflects the fact that constructing an egg chamber and oviposition are exclusively female behaviours. As a result, males would be better served by directing their care to alternative behaviours, such as delivering dung portions to the brood chamber. Sex-specific tasks may explain why in species where female parental roles are more critical towards the latter stages of offspring care, females are often left in the 'cruel bind' of remaining to provide investment once the male has deserted (Ridley 1978; Zeh & Smith 1985).

Our results also demonstrate sexual conflict over the way that the sexes differentially allocate their time between parental care and mating effort. In *O. taurus*, 52% of a male's time budget was allocated to paternity assurance behaviours and this time was traded against the male's ability to provide care. Elsewhere, we have found that the magnitude of this trade-off is directly related to the number of sneak males present, and thus a major male's confidence of paternity (Hunt & Simmons, in press). Similar trade-offs have been shown in a number of bird species, where participation in extrapair copulations (Houston & Davies 1985; Møller 1991; Markman et al. 1995, 1996; Freeman-Gallant 1998) and mate guarding (Leffelaar & Robertson 1986; Martin & Cooke 1987) are traded against a male's provisioning ability. Furthermore, studies on various passerine birds have shown that paternal care may be traded not only against mating effort but also against components of somatic maintenance (Slagsvold & Lifjeld 1989; Slagsvold et al. 1994; Slagsvold 1997; Svensson & Nilsson 1997; Hemborg & Merilä 1998; Hemborg 1999).

Our findings also show that a male's allocation to mating effort directly conflicts with a female's ability to provide care. In females, the primary nonparental behaviour was interacting with the male ( $13.5 \pm 1.7\%$ ), while grooming represented only a small proportion of her time budget ( $0.7 \pm 0.3\%$ ). The proportion of time males and females spent interacting, and the corresponding distribution of successful second matings, peaked immediately prior to oviposition. This resulted in a reduction in the proportion of time a female allocated to parental behaviours, the magnitude of which directly reflected the proportion of time the male spent interacting with the female (Figs 3, 4). In the dunnock, *Prunella modularis*, alpha males actively guard and chase females during their fertile period, to prevent neighbouring males from mating (Davies 1985). Such paternity assurance behaviours are costly to the female, decreasing her feeding rate and increasing the number of unhatched eggs in the nest (Davies 1985). Thus, a male's attempt to optimize his paternity appears to limit not only his own ability to provide care but also his partner's contribution.

### Compensatory Responses of Unassisted Females

Our findings contribute to an already extensive list of empirical studies showing that females are able to compensate for the removal of their partner (reviewed by Bart & Tornes 1989; Møller 2000), but represents one of the first to show such an effect in a taxon other than birds (but for fish see Timms & Keenleyside 1975; Mrowka

1982). In biparental birds, the majority of empirical studies have shown that female compensation is usually incomplete and that the absence of male care is often detrimental to offspring fitness (Alatalo et al. 1982; Leffelaar & Robertson 1986; Lyon et al. 1987; Wolf et al. 1988; Bart & Tornes 1989; Dunn & Hannon 1989; Whillans & Falls 1990; Meek & Robertson 1991; Dunn & Robertson 1992; Markman et al. 1996). In agreement with these findings, we have shown that unassisted females allocate proportionally more time to parental care than paired females. However, despite this increased investment, unassisted females did not completely compensate for the lack of a partner. Unassisted females performed fewer caring behaviours than pairs and as a result produced lighter brood masses. As brood mass weight is a major determinant of adult body size in *O. taurus* (Hunt & Simmons 1997) and size is directly related to reproductive fitness (Hunt & Simmons 2001), the inability of unassisted females to compensate completely for the lack of a partner will have important fitness consequences.

These results lead to the obvious question, why do unassisted females only partially compensate for the lack of a partner? Incomplete compensation is theoretically expected under ESS models of biparental cooperation, if unassisted females are working towards their independent optimum that is below that of a cooperative pair (Chase 1980; Houston & Davies 1985; Winkler 1987). Females provisioning without male assistance are expected to optimize their investment according to the trade-off between the benefits of investment to offspring fitness and the costs to future reproduction (Williams 1966). Experiments manipulating the fitness gains received from investment suggest that females are able to adjust their investment optimally in accordance with this trade-off (unpublished data). Furthermore, the level of investment provided by unassisted females is always below that of pairs (Hunt & Simmons 1998a, 2000) suggesting that the investment optimum of individuals in pairs is likely to exceed that of an unassisted female. However, an alternative explanation for incomplete compensation may be that unassisted females were physically unable to compensate for the loss of their partner. In birds, incomplete compensation is often the result of physical limitations caused by time constraints on the rate at which food can be gathered (Wright & Cuthill 1990a) or because unassisted females are already working at their physiological limit (Drent & Daan 1980). Clearly, more work is needed to determine the proximate mechanism involved in incomplete compensation by females. One potential avenue may be through the experimental manipulation of female condition and how this relates to the magnitude of female compensation.

### Coordinated Responses of the Sexes

The results of our breeding experiment clearly show that, irrespective of parental size, all cooperative pairs produced the same number of offspring and provided each offspring with the same amount of resources. This result is in qualitative agreement with our earlier findings that pairs containing major males of various sizes produce



the same number of brood masses of equal weight (Hunt & Simmons 2000). Since the weight of brood masses produced by unassisted females is positively related to female size (Hunt & Simmons 2000), cooperative pairs containing a small female must provide relatively more care to achieve this increased brood mass weight. We have shown that the increased brood mass weights produced by these pairs is the result of both the male and female working together in unison by providing more caring behaviours. Furthermore, contrary to the general theoretical prediction of a negative correlation between the level of care provided by the two members of a cooperative pair (Chase 1980; Houston & Davies 1985; Winkler 1987), we found that the level of care provided by the sexes in a cooperative pair was positively correlated.

A major limitation of Chase's (1980) ESS model is that it assumes that a parent responds to the contribution of its partner so as to maximize its own inclusive fitness, an assumption that may not have widespread biological appeal. However, in situations where parents coordinate their cooperative behaviours, each parent may receive greater fitness returns than it would acting independently, a process called reciprocal altruism (Trivers 1971). In this study, we have provided clear evidence that male *O. taurus* coordinate their parental behaviours with the female rather than acting independently. In situations where parents coordinate their efforts it is often more appropriate to view these actions as 'iterated games' (Maynard Smith 1982). In their original formulation, Axelrod & Hamilton (1981) modelled reciprocity as an iterated Prisoner's Dilemma game and showed that a simple Tit-for-Tat strategy, whereby an individual cooperates on its first move and then matches its partner's previous move, often prevailed over evolutionary time. While more recent developments have challenged the importance of this strategy (Boyd & Lorberbaum 1987; Axelrod & Dion 1988; Nowak 1990; Nowak & May 1992), each has shown that similar strategies may be evolutionarily stable if animals play stochastically (May 1987; Hirshleifer & Martinez Coll 1988; Boyd 1989) or if parents differ in their quality (Boyd 1992; Leimar 1997). An interesting outcome of such models is that when the probability of repeated interactions between parents is increased, individuals not only cooperate more but also develop greater generosity (Lazarus 1989; Sherratt & Roberts 1998). In *O. taurus*, the restriction of parents to a breeding tunnel ensures that they interact repeatedly during offspring provisioning and may provide the necessary conditions favouring the coordination of caring behaviours between the sexes.

Our findings directly contrast with the available empirical evidence on sexual compensation in birds. In the majority of biparental bird species, the parental effort provided by each sex in a cooperative pair is generally in agreement with the theoretical prediction of a negative correlation (Wright & Cuthill 1989, 1990a; Markman et al. 1995; Freeman-Gallant 1998). We suggest that one reason for our conflicting results may reflect differences in the type of parental care being provided by *O. taurus*. In onthophagine dung beetles, all offspring provisioning

is given prior to fertilization and oviposition and no subsequent care is provided once the brood mass has been completed (Halffter & Edmonds 1982). In contrast, birds provision their offspring after hatching and a number of empirical studies have shown that nestling begging plays a central role in regulating the provisioning rates of parents (Wright & Cuthill 1990a; Ottosson et al. 1997; Wright 1998; Wright & Dinglemanse 1999; Agrawal et al. 2001). As nestling begging provides a reliable signal of nestling hunger (Godfray 1991; Whittingham & Robertson 1993; Price & Ydenberg 1995; Cotton et al. 1996; Leonard & Horn 1996), parents are provided with a feedback mechanism with which to reduce their care adaptively if their partner has increased its effort to satisfy the demands of the nestlings. The lack of such a feedback mechanism in *O. taurus*, and the more general absence of overt parent-offspring interaction, may place a greater emphasis on interactions between parents in determining investment optima in this species.

### Acknowledgments

We thank Robert Black for bringing our attention to the Sony CCT video camera (XC-999P), which greatly improved the quality of our research. We also thank the McKay and Byrne families for continued access to their properties to collect dung and beetles, respectively. Janne Kotiaho and an anonymous referee provided comments that greatly improved the manuscript. J.H. was supported by an Australian Postgraduate Award and L.W.S. by the Australian Research Council.

### References

- Agrawal, A. F., Brodie, E. D. III & Brown, J. 2001. Parental-offspring coadaptation and the dual genetic control of maternal care. *Science*, **292**, 1710–1712.
- Alatalo, R. V., Lundberg, A. & S athlbrandt, K. 1982. Why do pied flycatcher females mate with already-mated males? *Animal Behaviour*, **30**, 585–593.
- Alatalo, R. V., Gottlander, K. & Lundberg, A. 1988. Conflict or cooperation between parents in feeding nestlings in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica*, **19**, 31–34.
- Axelrod, R. & Dion, D. 1988. The further evolution of cooperation. *Science*, **242**, 1385–1390.
- Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science*, **211**, 1390–1396.
- Bart, J. & Tornes, A. 1989. Importance of monogamous male birds in determining reproductive success: evidence for house wrens and a review of male-removal studies. *Behavioral Ecology and Sociobiology*, **24**, 109–116.
- B edard, J. & Meunier, M. 1983. Parental care in the Savannah sparrow. *Canadian Journal of Zoology*, **61**, 2836–2843.
- Boyd, R. 1989. Mistakes allow evolutionary stability in the repeated Prisoner's Dilemma game. *Journal of Theoretical Biology*, **136**, 47–56.
- Boyd, R. 1992. The evolution of reciprocity when conditions vary. In: *Coalitions and Alliances in Humans and other Animals* (Ed. by A. M. Harcourt & F. B. M. de Waal), pp. 473–489. Oxford: Oxford University Press.
- Boyd, R. & Lorberbaum, J. 1987. No pure strategy is evolutionarily stable in the repeated Prisoner's Dilemma game. *Nature*, **327**, 58–59.

- Chase, I. D. 1980. Cooperative and noncooperative behaviour in animals. *American Naturalist*, **115**, 827–857.
- Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.
- Cook, D. F. 1987. Sexual selection in dung beetles. 1. A multivariate study of the morphological variation in two species of dung beetle *Onthophagus* (Scarabaeidae: Onthophagini). *Australian Journal of Zoology*, **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). *Australian Journal of Zoology*, **36**, 521–532.
- Cotton, P. A., Kacelnick, A. & Wright, J. 1996. Chick begging as a signal: are nestlings honest? *Behavioural Ecology*, **7**, 178–182.
- Davies, N. B. 1985. Cooperation and conflict among dunnocks, *Prunella modularis*, in a variable mating system. *Animal Behaviour*, **33**, 628–648.
- Drent, D. H. & Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea*, **68**, 225–252.
- Dunn, P. O. & Hannon, S. J. 1989. Evidence for obligate male parental care in black-billed magpies. *Auk*, **106**, 635–644.
- Dunn, P. O. & Robertson, R. J. 1992. Geographic variation in the importance of male parental care and mating systems in tree swallows. *Behavioral Ecology*, **3**, 291–299.
- Emlen, D. J. 1996. Artificial selection on horn length-body size allometry in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Evolution*, **50**, 1219–1230.
- Freeman-Gallant, C. R. 1998. Fitness consequences of male parental care in Savannah sparrows. *Behavioral Ecology*, **9**, 486–492.
- Godfray, H. C. J. 1991. Signalling of need by offspring to their parents. *Nature*, **352**, 328–330.
- Goldstein, H. & Yom-Tov, Y. 1988. Breeding biology of the orange-tufted sunbird in Israel. *Ardea*, **68**, 169–174.
- Greenlaw, J. S. & Post, W. 1985. Evolution of monogamy in seaside sparrows, *Ammodramus maritimus*: tests of hypotheses. *Animal Behaviour*, **33**, 373–383.
- Halfpter, G. & Edmonds, W. G. 1982. *The Nesting Behaviour of Dung Beetles (Scarabaeidae): An Ecological and Evolutionary Approach*. Mexico: Instituto de Ecología.
- Hemborg, C. 1999. Sexual differences in moult-breeding overlap and female reproductive costs in pied flycatchers, *Ficedula hypoleuca*. *Journal of Animal Ecology*, **68**, 429–436.
- Hemborg, C. & Merilä, J. 1998. A sexual conflict in collared flycatchers, *Ficedula albicollis*: early male moult reduces female fitness. *Proceedings of the Royal Society of London, Series B*, **265**, 2003–2007.
- Hirshleifer, J. & Martinez Coll, J. C. 1988. What strategies can support the evolutionary emergence of cooperation? *Journal of Conflict Research*, **32**, 367–398.
- Holstein, V. 1942. *Duehagen*. Copenhagen: Hirschsprung.
- Houston, A. I. & Davies, N. B. 1985. The evolution of cooperation and life history in the dunnock *Prunella modularis*. In: *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (Ed. by R. M. Sibley & R. H. Smith), pp. 471–487. Oxford: Blackwell Scientific.
- Hunt, J. & Simmons, L. W. 1997. Patterns of fluctuating asymmetry in beetle horns: an experimental examination of the honest signalling hypothesis. *Behavioral Ecology and Sociobiology*, **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). *Behavioural Ecology and Sociobiology*, **42**, 447–451.
- Hunt, J. & Simmons, L. W. 1998b. Patterns of fluctuating asymmetry in beetle horns: no evidence for reliable signalling. *Behavioral Ecology*, **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*. *Proceedings of the Royal Society of London, Series B*, **268**, 2409–2914.
- Hunt, J. & Simmons, L. W. In press. Confidence of paternity and paternal care: covariation revealed through experimental manipulation of a mating system in the beetle *Onthophagus taurus*. *Journal of Evolutionary Biology*.
- Kemp, A. C. 1988. Hornbills. In: *The Birds of North America*. Vol. 13 (Ed. by C. H. Keith & E. K. Urban), pp. 375–413. Washington: American Ornithologists Union.
- Lazarus, J. 1989. The logic of mate desertion. *Animal Behaviour*, **39**, 672–684.
- Lee, J. M. & Peng, Y. S. 1982. Influence of manure availability and nesting density on the progeny size of *Onthophagus gazella*. *Environmental Entomology*, **11**, 38–41.
- Leffelaar, D. & Robertson, R. J. 1986. Equality of feeding roles and the maintenance of monogamy in tree swallows. *Behavioral Ecology and Sociobiology*, **18**, 199–206.
- Leimar, O. 1997. Reciprocity and communication of partner quality. *Proceedings of the Royal Society of London, Series B*, **264**, 1209–1215.
- Leonard, M. & Horn, A. 1996. Provisioning rules in tree swallows. *Behavioral Ecology and Sociobiology*, **38**, 341–347.
- Lozano, G. A. & Lemon, R. E. 1996. Male plumage, paternal care and reproductive success in yellow warblers, *Dendroica petechia*. *Animal Behaviour*, **51**, 265–272.
- Lyon, B. E., Montgomerie, R. D. & Hamilton, L. D. 1987. Male parental care and monogamy in snow buntings. *Behavioral Ecology and Sociobiology*, **20**, 377–382.
- Markman, S., Yom-Tov, Y. & Wright, J. 1995. Male parental care in the orange-tufted sunbird: behavioural adjustments in provisioning and nest guarding effort. *Animal Behaviour*, **50**, 655–669.
- Markman, S., Yom-Tov, Y. & Wright, J. 1996. The effect of male removal on female parental care in the orange-tufted sunbird. *Animal Behaviour*, **52**, 437–444.
- Martin, K. & Cooke, F. 1987. Bi-parental care in willow ptarmigan: a luxury? *Animal Behaviour*, **35**, 369–379.
- May, R. M. 1987. More evolution of cooperation. *Nature*, **327**, 15–17.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Meek, S. B. & Robertson, R. J. 1991. Adoption of young by replacement male birds: an experimental study of eastern bluebirds and a review. *Animal Behaviour*, **42**, 813–820.
- Moczek, A. P. 1999. Facultative paternal investment in the polyphenic beetle *Onthophagus taurus*: the role of male morphology and social context. *Behavioral Ecology*, **10**, 641–647.
- Møller, A. P. 1991. Defence of offspring by male swallows, *Hirundo rustica*, in relation to participation in extra-pair copulations by their mates. *Animal Behaviour*, **42**, 261–267.
- Møller, A. P. 2000. Male parental care, female reproductive success and extra-pair paternity. *Behavioral Ecology*, **11**, 161–168.
- Mrowka, W. 1982. Effect of removal of the mate on the parental care behaviour of the biparental cichlid *Aequidens paraguayensis*. *Animal Behaviour*, **30**, 295–297.
- Mudal, A. M., Moffatt, J. D. & Robertson, R. J. 1986. Parental care of nestlings by male red-winged blackbirds. *Behavioral Ecology and Sociobiology*, **19**, 105–114.
- Mumme, R. L. & De Queiroz, A. 1985. Individual contributions to cooperative behaviour in the acorn woodpecker: effects of reproductive status, sex and group size. *Behaviour*, **95**, 290–313.
- Nowak, M. 1990. An evolutionarily stable strategy may be inaccessible. *Journal of Theoretical Biology*, **142**, 237–241.

- Nowak, M. & May, R. M. 1992. Evolutionary games and spatial chaos. *Nature*, **359**, 826–829.
- Ottoesson, U., Bäckman, J. & Smith, H. G. 1997. Begging affects parental effort in the pied flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology and Sociobiology*, **41**, 381–384.
- Price, K. & Ydenberg, R. 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. *Behavioral Ecology and Sociobiology*, **37**, 201–208.
- Quinn, J. S. 1990. Sexual size dimorphism and parental care patterns in a monomorphic and dimorphic larid. *Auk*, **274**, 260–275.
- Ridley, M. 1978. Parental care. *Animal Behaviour*, **26**, 904–932.
- Saino, N. & Møller, A. P. 1995. Testosterone-induced depression of male parental behaviour in the barn swallow: female compensation and effects on seasonal fitness. *Behavioral Ecology and Sociobiology*, **36**, 151–157.
- Sasvარი, L. 1990. Feeding responses of mated and widowed bird parents to fledglings: an experimental study. *Ornis Scandinavica*, **21**, 287–292.
- Sherratt, T. N. & Roberts, G. 1998. The evolution of generosity and choosiness in cooperative exchanges. *Journal of Theoretical Biology*, **193**, 167–177.
- Slagsvold, T. 1997. Is there a sexual conflict over hatching asynchrony in American robins. *Auk*, **114**, 593–600.
- Slagsvold, T. & Lifjeld, J. T. 1989. Hatching asynchrony in birds: the hypothesis of sexual conflict over parental investment. *American Naturalist*, **134**, 239–253.
- Slagsvold, T. & Lifjeld, J. T. 1990. Influence of male and female quality on clutch size in tits (*Parus* spp.). *Ecology*, **71**, 1258–1266.
- Slagsvold, T., Amundsen, T. & Dale, S. 1994. Selection by sexual conflict for evenly spaced offspring in blue tits. *Nature*, **370**, 136–138.
- Smith, H. G., Källander, H., Fontell, K. & Ljungström, M. 1988. Feeding frequency and parental division of labour in the double-brooded great tit *Parus major*. *Behavioural Ecology and Sociobiology*, **22**, 447–453.
- Smith, J. N. M., Yom-Tov, Y. & Moses, R. 1982. Polygyny, male parental care and sex ratio in song sparrows: an experimental study. *Auk*, **99**, 555–564.
- Sowig, P. 1996. Duration and benefits of biparental brood care in the dung beetle *Onthophagus vacca* (Coleoptera: Scarabaeidae). *Ecological Entomology*, **21**, 81–86.
- Svensson, E. & Nilsson, J. 1997. The trade-off between molt and parental care: a sexual conflict in the blue tit. *Behavioral Ecology*, **8**, 92–98.
- Timms, A. M. & Keenleyside, M. H. A. 1975. The reproductive behaviour of *Aequidens paraguayensis* (Pisces, Cichlidae). *Zeitschrift für Tierpsychologie*, **39**, 8–23.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35–57.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.
- Weatherhead, P. J. 1979. Ecological correlates of monogamy in tundra-breeding savannah sparrows. *Auk*, **96**, 391–401.
- Westneat, D. F. & Sargent, R. C. 1996. Sex and parenting: the effects of sexual conflict and parentage on parental strategies. *Trends in Ecology and Evolution*, **11**, 87–91.
- Whillans, K. V. & Falls, J. B. 1990. Effects of male removal on parental care of female white-throated sparrows, *Zonotrichia albicollis*. *Animal Behaviour*, **39**, 869–878.
- Whittingham, L. A. & Robertson, R. 1993. Nestling hunger and parental care in red-winged blackbirds. *Auk*, **110**, 240–246.
- Williams, G. C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. *American Naturalist*, **100**, 687–690.
- Winkler, D. W. 1987. A general model for parental care. *American Naturalist*, **130**, 526–543.
- Wolf, L., Ketterson, E. D. & Nolan, V. Jr 1988. Paternal influence on growth and survival of dark-eyed junco young: do parental male benefit? *Animal Behaviour*, **36**, 1601–1618.
- Wolf, L., Ketterson, E. D. & Nolan, V. Jr 1990. Behavioural response of female dark-eyed juncos to the experimental removal of their mates: implications for the evolution of male parental care. *Animal Behaviour*, **39**, 125–134.
- Wright, J. 1998. Helpers-at-the-nest and group size in the Arabian babbler (*Turdoides squamiceps*). *Journal of Avian Biology*, **29**, 105–111.
- Wright, J. & Cuthill, I. 1989. Manipulation of sex differences in parental care. *Behavioral Ecology and Sociobiology*, **25**, 171–181.
- Wright, J. & Cuthill, I. 1990a. Manipulation of sex differences in parental care: the effect of brood size. *Animal Behaviour*, **40**, 462–471.
- Wright, J. & Cuthill, I. 1990b. Biparental care: short term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris*. *Behavioral Ecology*, **1**, 116–124.
- Wright, J. & Dinglemanse, N. J. 1999. Parents and helpers compensate for experimental changes in the provisioning effort of others in the Arabian babbler. *Animal Behaviour*, **58**, 345–350.
- Zar, J. H. 1985. *Biostatistical Analysis*. Upper Saddle River, New Jersey: Prentice Hall.
- Zeh, D. W. & Smith, R. L. 1985. Parental investment by terrestrial arthropods. *American Zoologist*, **25**, 785–805.