Negotiation between parents over care: reversible compensation during incubation

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Parental care is often beneficial for the young but costly for the caregiving parent. Because both parents benefit from care via the offspring, whereas they pay the costs individually, a conflict is expected about how much care each parent should provide. How do parents settle this conflict? We addressed this question by reducing nest temperatures during incubation in the Kentish plover Charadrius alexandrinus, a small ground-nesting shorebird in which the parents share incubation. By cooling the nest and recording the behavioral responses of the targeted parent and its mate. Unlike most previous manipulations of parental effort, our manipulation sought to measure a parent’s response to an increase, not a shortfall, in the partner’s contribution. The manipulation was also short term and reversed between the members of a given pair. We found that there is a trade-off between the efforts of parents because increased (or reduced) effort by the targeted parent was associated with decreased (or increased) effort by its mate, respectively. This result is consistent with theoretical models that predict compensation as a response to changed parental effort of the mate. We also found that compensation was consistent between treatments when the male or the female of a given pair was targeted. Furthermore, our results support the notion that parents adjust their effort in response to their mate’s behavior in real time, that is, they negotiate parental roles. Key words: parental care, precocial bird, sexual conflict, shorebird, wader.

Bi-parental care of young is an excellent model system for investigating cooperation and conflict between unrelated individuals. On the one hand, cooperation between parents is beneficial because provisioning the eggs and young with nutrients, defending them from predators and training them in useful skills usually improve the offspring’s chances of survival and reproduction (Clutton-Brock 1991; Balshine et al. 2002). On the other hand, parental care is costly because it takes time and energy and the caring parent may be taken by predators (Lessells 1999; Houston et al. 2005). Finding the outcome of these conflicting selective forces is not straightforward because the benefits are shared between the parents, via the offspring, whereas each parent pays the costs itself. The existence of biparental care in insects, fishes, frogs, birds, and mammals thus provides excellent opportunities to test hypotheses about how conflict and cooperation influence social behavior (Trivers 1972; Parker et al. 2002).

How do parents settle their conflict? The influential model by Houston and Davies (1985) used provisioning rates of parents and predicted partial compensation; that is, if one parent increases its effort, the other parent should decrease its effort by a lesser extent. However, in Houston and Davies (1985), parents do not adjust their work rate in response to the behavior of their mate in real time but their strategy is fixed in evolutionary time (a “sealed bid” in game theoretic terminology). Models that incorporate repeated decisions of the parents (negotiation) predict either compensation (McNamara et al. 1999) or responses ranging from compensation to matching, that is, an increase in work rate in response to an increase by the mate (Taylor and Day 2004; Johnstone and Hinde 2006).

Numerous experiments have been carried out to test the predictions of such models in birds, insects, fish, and mammals. Two major approaches have been used to test the responses of parents to changed effort by their mate: 1) mate removal (e.g., Erckmann 1983; Martin and Cooke 1987; Alatalo et al. 1988; Markman et al. 1996; Smiseth and Amundsen 2000) and 2) handicapping (attaching extra weights or clipping feathers, e.g., Wright and Cuthill 1989; Slagsvold and Lifjeld 1990; Markman et al. 1995; Sanz et al. 2000). The results of these experiments have been contradictory because parents responded variably to the changed work rate of their mate by compensation or matching, whereas in some studies, no significant response was detected (reviewed by Bart and Tornes 1989; Sanz et al. 2000; Houston et al. 2005; Smiseth et al. 2005; Hinde 2006). These experiments, however, are limited in what can be deduced about the negotiation process (if one exists), in that the manipulation usually lasted over several days of the care period and in each pair only a single parent was manipulated.

Here, we investigate the responses of parents to changed effort by their partner in a small shorebird (body mass: 40–44 g), the Kentish plover Charadrius alexandrinus, in which the parents share incubation. The sexes have different incubation patterns: The males incubate mostly during the night, whereas females do most of the daylight incubation (Rittinghaus 1961; Fraga and Amat 1996; Kosztolányi and Székely 2002). After hatching of the chicks, one parent (usually the female) may desert the brood, thus brood care is variable in most populations: Biparental, male-only, and female-only care may all occur in a single population (Lessells 1984; Warriner et al. 1986; Amat et al. 1999; Kosztolányi et al. 2006).

To manipulate incubation effort in the Kentish plover, we increased the workload of parents by cooling the nest and the eggs using a remotely controlled device. Our experiment...
is novel for 2 reasons. First, we used short-term manipulations (hours), whereas previous studies of parental interactions employed long-lasting manipulations (days, weeks; by removing the mate or attaching extra weights or clipping feathers). The advantage of our approach is that we can separate effects during and after manipulations. Second, males and females of each pair were manipulated on different days in random order, that is, we reversed the manipulations between members of a given pair. This has not been done in previous studies, except Hinde (2006) used playback of begging calls to reversibly manipulate care by male and female great tits *Parus major*.

We had 2 major objectives. First, to test how parents respond to an increased workload during incubation. Second, to test how males and females respond to a changed level of parental effort of their mate. Unlike most avian studies of parental effort, 1) we manipulated the parental behavior during incubation and not during brood care and 2) we aimed to increase and not decrease the effort of the manipulated parent. During incubation, the costs of parental absence, and thus the joint commitment to care, may differ from during chick feeding (e.g., prolonged absence may lead to embryo death rather than retarded growth). An advantage of targeting incubation is that offspring behavior during incubation is unlikely to confound the outcome of the negotiation between the parents (Parker et al. 2002; Johnstone and Hinde 2006) because in behavioral (though not evolutionary) terms an egg is a more passive player in the game than a chick. A further difference between brood care and incubation in the context of parental care is that during brood care, the parents can independently increase the contribution to chick feeding, whereas during incubation, an increase in incubation time by one parent is only possible if the other member of the pair is not sitting on, or can be persuaded to leave, the nest.

**MATERIALS AND METHODS**

**Study area and field methods**

The experiment was carried out at Al Wathba Wetland Reserve (24°15.5′N, 54°36.2′E) in the United Arab Emirates about 40 km southeast from Abu Dhabi in 2 years: 2005 (23 March–19 June) and 2006 (26 April–12 July). The Reserve is 3.7 km long and 1.9 km wide, the total area is about 450 ha, and it is composed of natural and man-made water bodies with sand dunes separating the water bays of the lakes.

To study incubation behavior and manipulate the thermal condition of the nest, an automatic nest monitoring system was developed (Figure 1). The system consisted of 4 main parts. First, an electronic balance (Navigator, Ohaus Corporation, Pine Brook, NJ) was placed under the nest scrape and connected to a data logger (Gigalog, Audon Electronics, Nottingham, UK) to record the body mass of the incubating parent every 20 s. The nest was placed on a plastic tray on top of the balance. The extreme ambient temperature (see below) and strong wind, however, made the readings of the balance unreliable, so these measurements were not investigated further. Second, a thermoprobe was inserted into the bottom of the nest scrape and another probe about 25 cm from the nest scrape at ground level to measure the thermal condition of the nest and the environment, respectively. The probes were connected to a data logger (Tinytag, Gemini Data Loggers Ltd, Chichester, UK) that recorded data every 20 s. Third, a small spy camera (Outdoorcam, Swann Communications Pty. Ltd, Richmond, Victoria, Australia) was positioned about 1 m from the nest and connected to a digital video recorder (MemoCam, Video Domain Technologies Ltd, Petah Tikva, Israel) to record the behavior of the parents every 20 s. The camera had infrared light sources that allowed recording of behavior at night. The plumage of adult Kentish plovers is sexually dimorphic during the breeding season, and this allows identification of sexes from the photos. Fourth, a Peltier heat pump (RS Components Ltd, Corby, UK) was placed under the nest scrape to change the thermal condition of the nest. This device was connected to a central unit that was remote controlled. The power was supplied by a car battery. All parts of the system (except the camera) and the cables were hidden underground to minimize the disturbance to the plovers.

The experiment lasted for 4 days at each nest. Before the experiment, both parents were captured, measured, and color ringed. All experimental nests had 3 eggs (modal clutch size), and the clutches were 11.9 ± 1.02 days old (mean ± standard error [SE], n = 20) at the start of the experiment. On the first day, the system was set up at the nest, the second day was a baseline, and on the third and fourth days, we cooled the nest between either 22:00 and 04:00 or 05:00 and 09:00 to target the male or female, respectively (Figure 2). The order of cooling was randomized at a nest. The system was visited daily to change memory cards in data loggers, to change the balance. The extreme ambient temperature (see below) every day was taken and data from the first baseline day were omitted.

Data were collected by 2 nest monitoring systems at 20 nests in total. Three nests were predated while the experiment was running; therefore, data are missing for 3 female manipulation days. At 3 different nests, the parents delayed returning to the nest after setting up the system; at these nests, an extra baseline day was taken and data from the first baseline day were omitted.

We expected that the parents aim to mitigate the effect of cooling on egg temperatures. To assess the effect of cooling...
on nest temperature without the parents, we measured nest and ambient temperatures at 5 unused nests ("dummy nests" henceforward; 3 nests in 2005 and 2 in 2006). In these cases, the nest monitoring system was set up at previously predated, abandoned, or hatched Kentish plover nests for 1 day, and 3 fresh eggs of Japanese quail Coturnix japonica were cooled for equivalent periods for the male and female manipulation (22:00–04:00 or 05:00–09:00, respectively). The quail egg is similar in size and shape to the Kentish plover egg.

Statistical analyses

We considered each nest as the unit of analysis. The effect of manipulation on incubation behavior was measured by the change in incubation time (%, i.e., percentage of incubation during manipulation day minus percentage of incubation during baseline day). The baseline and manipulation days were divided into 2 parts: manipulation period (22:00–04:00 and 05:00–09:00 for male and female manipulation day, respectively) and after manipulation period (04:00–10:00 and 09:00–13:00 for male and female manipulation day, respectively). The responses by the male and female during and after manipulation were not influenced significantly by year, by the nest monitoring system (set 1 or set 2) used for data collection and manipulation, or by the order of manipulation (analyses of variance, \( P \geq 0.194 \) in all cases); therefore, these effects were not considered in further analyses.

With the 22:00–04:00 manipulation period, we targeted the male, whereas with the 05:00–09:00 period, the female parent was targeted. However, the targeted parent did not always incubate during the whole cooling period (see below); thus, the amount of manipulation experienced by a given parent depended on the time it spent on the nest during manipulation. Therefore, we used a covariate \((\Delta T)\) in the linear models to investigate the effect of manipulation on the response of the sexes. \(\Delta T\) for a given sex was defined as the absolute value of the effect of cooling on nest temperature \((T_{\text{nest}} - T_{\text{ambient}})\) multiplied by the time the parent was incubating the nest during the cooling period. The effect of cooling for a given day of the season was estimated by using the temperature data of dummy nests (see below).

The presence of parents influenced the effect of cooling because the difference between nest and ambient temperature \((T_{\text{nest}} - T_{\text{ambient}})\) was smaller at experimental nests than at dummy nests (22:00–04:00, experimental nests: \(-1.2 \pm 0.27 ^\circ\text{C}\), dummy nests: \(-4.2 \pm 0.52 ^\circ\text{C}\); \( t_{23} = 4.924, P < 0.001; 05:00–09:00, experimental nests: \(-3.3 \pm 0.25 ^\circ\text{C}\), dummy nests: \(-5.9 \pm 0.32 ^\circ\text{C}\); \( t_{20} = 5.245, P < 0.001\)). Furthermore, the effect of cooling \((\text{i.e., } T_{\text{nest}} - T_{\text{ambient}})\) at dummy nests tended to be larger in absolute value over the breeding season (least squares regressions, male manipulation: \( B = -0.02 \pm 0.021; \ t_{5} = 1.157, P = 0.331\); female manipulation: \( B = -0.02 \pm 0.007; \ t_{5} = 3.552, P = 0.038\)). Therefore, the manipulations received by the sexes \((\Delta T)\) were estimated using temperature difference \((T_{\text{nest}} - T_{\text{ambient}})\) estimated for a given date using the coefficients of the above least squares regressions.

During male-targeted manipulations, the male was on the nest 70.2 ± 5.06% of the time (mean ± SE), the female 26.2 ± 4.71%, and neither parent 3.6 ± 0.71%. That is, males spent more time on the nest than females when males were targeted (paired \( t\)-test, \( t_{5} = 4.522, P < 0.001\)). In contrast, during female-targeted manipulations, the females spent more time on the nest than males \((t_{5} = 11.525, P < 0.001); \) male: 9.1 ± 2.84%, female: 77.3 ± 3.41%, neither: 13.6 ± 2.10%). Thus, during male-targeted manipulations, the males experienced more cooling than females \((\Delta T_{\text{male}} = 17.5 \pm 1.34 ^\circ\text{C} \times h, \Delta T_{\text{female}} = 5.8 \pm 1.28 ^\circ\text{C} \times h; \) paired \( t\)-test, \( t_{5} = 4.321, P < 0.001\)), whereas during female-targeted manipulations, females experienced more cooling than males \((\Delta T_{\text{male}} = 2.1 \pm 0.69 ^\circ\text{C} \times h, \Delta T_{\text{female}} = 18.2 \pm 0.94 ^\circ\text{C} \times h; \) \( t_{5} = 10.694, P < 0.001\)). This is, of course, what the experiment was designed to achieve, but we stress that “male” and “female” targeting was a statistical, not deterministic, difference because sometimes the “wrong” sex was present and experienced the manipulation targeted at its mate.

One may argue that the responses of parents may depend on their original effort; for instance, if a parent is already incubating 90% of its time, it is less likely to increase its incubation as a response to manipulation than a parent that incubates only 10% of its time (a “ceiling effect”). We investigated this proposition by weighting the response as \(\exp(x/100)\) when \( x\) that is, the change in incubation time was a positive response and \(\exp(1 - x/100)\) when \( x\) was negative. However, applying weights does not change our conclusions, so these results are not reported.

We used vectors to analyze the responses of parents to their mate’s behavior. The baseline period was taken as the origin, and the coordinates represented changes in male and female incubation compared with the baseline period. Thus, a vector captured the joint change in the level of incubation of the male and female in a given pair. In one pair, incubation did not change during the male manipulation period compared with the baseline (i.e., the length of the vector was zero), therefore this nest was not considered during the male manipulation period.

To investigate the distribution of vectors, we divided the parameter space into 2 triangles along the male change = female change (+1 slope) line (isocline, henceforward). Vectors between 0° and 45° either side of the isocline mean that both parents increased incubation (“matching,” see Figure 3); vectors between 45° and 135° mean that one parent increased incubation while the other decreased (“compensation” by the female or the male; upper left and lower right triangles, respectively), whereas vectors between 135° and 180° mean that both parents decreased incubation (“negative matching”).

We investigated the behavioral responses in vector space in 3 ways. First, we used the absolute deviation of vectors from the isocline and calculated the mean deviation and their 95% confidence intervals (CI). Second, we also considered the length of the vectors and calculated the mean vector and the 95% confidence area for the altered level of incubation separately for the 2 triangles. Finally, to compare the responses of pairs between male and female manipulations, we used the absolute deviation of vectors from the isocline.

Figure 2
The effects of cooling on internal nest temperature (solid line) and the ambient ground temperature (broken line) at an experimental nest. In this example, the first cooling targeted the male and the second cooling the female.
Statistical analyses were carried out using R 2.6.0 (R Development Core Team 2007). Values are given as mean ± SE unless indicated otherwise.

RESULTS

Effect of manipulation on incubation behavior

Cooling of the eggs influenced parental behavior: Total incubation was higher during male manipulation than during baseline periods, and total incubation increased with the cooling the parents experienced (Table 1). Males, but not females, increased their incubation time with the manipulation they received (regression on ΔT). After manipulation, male incubation nonsignificantly tended to decrease, whereas female incubation increased compared with the baseline day (Table 1). Similar to the preceding results, total incubation was higher during female manipulation than during baseline (Table 1). Furthermore, incubation by females, but not males, was higher during the manipulation than baseline (Table 1). After female manipulation, total incubation was significantly higher in nests that had previously received more cooling (regression on ΔT), but no other relationships after female manipulation were significant (Table 1). The nonsignificant trend was for females to decrease incubation and for males to increase after female manipulation.

Although these results show that the manipulation had an effect on parental behavior, they cannot explain how a parent responded to the changed effort of its mate because here males and females were tested independently. Furthermore, the slopes on ΔT are not comparable between the sexes because the ranges of the explanatory variable (i.e., the amount of manipulation received) were different between males and females (see Materials and Methods).

Response to mate’s behavior

Compensation by the mate, rather than matching, was the most common response to the manipulation. First, during
The 2 parents spent on the nest was significantly different from mean vectors and their confidence areas were largely restricted (upper left triangle) or almost restricted (lower right triangle) to the compensation areas (male manipulation–mean: 85.7, 95% CI: 64.9–106.5, n = 16; female manipulation–mean: 90.4, 95% CI: 76.9–103.9, n = 17). Furthermore, both the mean vectors and their confidence areas were largely restricted to the compensation areas (Figure 3).

Third, after manipulations, the responses of the parents with respect to each other were similar to the ones during manipulations because the mean angle of vectors were inside the compensation area for male manipulation—mean: 85.7°, 95% CI: 64.9°–106.5°, n = 20; female manipulation—mean: 90.4, 95% CI: 76.9–103.9, n = 17). Furthermore, both the mean vectors and their confidence areas were largely restricted to the compensation areas (Figure 3).

It is unlikely that the compensatory responses were due to an upper limit in total incubation because the percentage of time the 2 parents spent on the nest was significantly different from 100% during the manipulation and after manipulation periods on both manipulation days (during male manipulation: 96.4 ± 0.71%, t45 = 5.052, P < 0.001; after male manipulation: 85.5 ± 1.68%, t45 = 8.626, P < 0.001; during female manipulation: 86.4 ± 2.10%, t45 = 6.471, P < 0.001; after female manipulation: 94.0 ± 1.99%, t45 = 3.059, P = 0.008, see also Materials and Methods for a summary of ceiling effect analyses).

**DISCUSSION**

Our experiment provided 3 key results. First, Kentish plover parents responded to the changed level of incubation of their partner in real time, a result consistent with negotiating parental roles (sensu McNamara et al. 1999). Thus, our results of the manipulation of parental workload during incubation are in line with the results of most experimental manipulations of parental effort during brood rearing of birds. Most studies have also found real-time responses to the change in parental effort by the mate (e.g., Wright and Coulthill 1989; Markman et al. 1995; Sanz et al. 2000), whereas few have supported the sealed bid notion (Schwagmeyer et al. 2002 and references therein). The reason for these intriguing interspecific differences in negotiation strategies remains unknown.

Second, we showed that compensation, rather than matching, was the most common response by Kentish plover parents to cooling of the eggs (or the partner’s response to cooling).

The opponents of the compensation notion aimed at increasing the contribution of the targeted parents (cf., handicapping and removal), and we did achieve this because total incubation increased during both manipulation...
periods compared with the baseline day. When one parent increased its incubation time in response to egg cooling, the response of the partner usually failed to keep its own effort constant, or matched it, but to decrease it. The latter result suggests that there is a conflict between the parents over the amount of parental effort and that each parent tries to avoid the costs of parental care and shunt the work on its partner (Houston et al. 2005). Some of our results indicate overcompensation (e.g., increasing total incubation). These results are intriguing because they are not in line with the results of most previous experiments and the predictions of theoretical models. However, our results are not comparable to previous studies because we aimed at increasing the effort of the manipulated parents.

Third, the parents’ responses were consistent during the manipulation and after manipulation periods because most pairs exhibited compensation during all 4 periods. This consistency strengthens the suggestion that the actual changes in parental effort are results of a negotiation process.

To our knowledge, the only experimental study on parental effort that, similarly to our study, has aimed at increasing the contribution of the targeted parent was Hinde (2006). Using playback of begging calls to modulate feeding rate in great tits, she showed matching rather than compensation between parents. The reason for these contrasting results may lie in the differences in information available for the parents because the information the parents have on the need or value of offspring may profoundly influence whether compensation or matching is the outcome of the negotiation process (Johnstone and Hinde 2006). Our results are in line with the predictions of Johnstone and Hinde (2006) because compensation is expected if the parents have reliable and symmetric information about the need of the offspring, which in the Kentish plover may be the difference between the optimal and actual egg temperature. In contrast, in Hinde (2006), the great tit parents may have used the mate’s increased work rate as a cue of increased brood need or quality, and they responded by matching, as predicted by Johnstone and Hinde (2006), if the parents have only partial information regarding brood need and quality.

The trade-off between male and female parental effort observed in this study has also been seen in comparative studies. Olson et al. (2008) showed, using parental care data from 193 bird species, a negative relationship between male and female care (for a similar result in shorebirds, see Thomas et al. 2007). These results are consistent with the proposition that there is an evolutionary tug-of-war between the sexes over who should care for the young, and although there is no necessary relationship between evolutionary and behavioral responses, this conflict may also be manifested during real-time behavioral decisions.

In conclusion, we have shown that parents rapidly and consistently respond to the changed effort of their mate in a ground-nesting shorebird, the Kentish plover, during incubation. We have also shown a trade-off between the parental effort by males and females (compensation). However, we do not know the limits of the compensatory response. That is, how far the pairs can be moved from their negotiated effort before failing to compensate and, for example, deserting the nest. To reveal the stability of the compensatory response, repeated manipulations of the same individuals with different levels of manipulations (e.g., variable amount of cooling) is needed.

REFERENCES


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