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## 24 **Summary**

25 Parental care is often beneficial for the young, but costly for the care-giving parent.  
26 Since both parents benefit from care via the offspring, whereas they pay the costs  
27 individually, a conflict is expected about how much care each parent should provide.  
28 How do parents settle this conflict? We addressed this question by reducing nest  
29 temperatures during incubation in the Kentish plover *Charadrius alexandrinus*, a small  
30 ground-nesting shorebird in which the parents share incubation. By cooling the clutch  
31 using a remote-controlled device built under the nest we experimentally increased the  
32 workload of either the male or the female in random order, and recorded the behavioral  
33 responses of the targeted parent and its mate. Unlike most previous manipulations of  
34 parental effort, our manipulation sought to measure a parent's response to an increase,  
35 not a shortfall, in the partner's contribution. The manipulation was also short-term and  
36 reversed between the members of a given pair. We found that there is a trade-off  
37 between the efforts of parents, since increased (or reduced) effort by the targeted parent  
38 was associated with decreased (or increased) effort by their mate, respectively. This  
39 result is consistent with theoretical models that predict compensation as a response to  
40 changed parental effort of the mate. We also found that compensation was consistent  
41 between treatments when the male or the female of a given pair was targeted.  
42 Furthermore, our results support the notion that parents adjust their effort in response to  
43 their mate's behavior in real time, i.e. they negotiate parental roles.

44 **Keywords:** sexual conflict, parental care, precocial bird, wader, shorebird

45 **Short title:** Parental negotiation during incubation

## 46 **Introduction**

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

59       How do parents settle their conflict? The influential model by Houston & Davies  
60 (1985) used provisioning rates of parents and predicted partial compensation; that is, if  
61 one parent increases its effort, the other parent should decrease its effort by a lesser  
62 extent. However, in Houston & Davies (1985) parents do not adjust their work rate in  
63 response to the behavior of their mate in real time, but their strategy is fixed in  
64 evolutionary time (a 'sealed bid' in game theoretic terminology). Models that  
65 incorporate repeated decisions of the parents ('negotiation') predict either compensation  
66 (McNamara et al. 1999), or responses ranging from compensation to matching, i.e. an  
67 increase in work rate in response to an increase by the mate (Taylor & Day 2004,  
68 Johnston & Hinde 2006).

69 Numerous experiments have been carried out to test the predictions of such models,  
70 in birds, insects, fish and mammals. Two major approaches have been used to test the  
71 responses of parents to changed effort by their mate: (i) mate removal (e.g. Erckmann  
72 1983, Martin & Cooke 1987, Alatalo et al. 1988, Markman et al. 1996, Smiseth &  
73 Amundsen 2000), and (ii) handicapping (attaching extra weights or clipping feathers,  
74 e.g. Wright & Cuthill, 1989, Slagsvold & Lifjeld 1990, Markman et al. 1995, Sanz et al.  
75 2000). The results of these experiments have been contradictory, since parents  
76 responded variously to the changed work rate of their mate by compensation or  
77 matching, whereas in some studies no significant response was detected (reviewed by  
78 Bart & Tornes 1989, Sanz et al. 2000, Smiseth et al. 2005, Houston et al. 2005, Hinde  
79 2006). These experiments, however, are limited in what can be deduced about the  
80 negotiation process (if one exists), in that the manipulation usually lasted over several  
81 days of the care period, and in each pair only a single parent was manipulated.

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

91 To manipulate incubation effort in the Kentish plover we increased the workload of  
92 parents by cooling the nest and the eggs using a remotely controlled device. Our

93 experiment is novel for two reasons. First, we used short-term manipulations (hours)  
94 whereas previous studies of parental interactions employed long-lasting manipulations  
95 (days, weeks; by removing the mate, or attaching extra weights or clipping feathers).  
96 The advantage of our approach is that we can separate effects during and after  
97 manipulations. Second, males and females of each pair were manipulated on different  
98 days in random order, i.e. we reversed the manipulations between members of a given  
99 pair. This has not been done in previous studies, except Hinde (2006) used playback of  
100 begging calls to reversibly manipulate care by male and female great tits *Parus major*.

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

## 117 **Material and methods**

### 118 **Study area and field methods**

119 The experiment was carried out at Al Wathba Wetland Reserve (24° 15.5' N, 54° 36.2'  
120 E) in the United Arab Emirates about 40 km south-east from Abu Dhabi, in two years:  
121 2005 (23 March – 19 June) and 2006 (26 April – 12 July). The Reserve is 3.7 km long  
122 and 1.9 km wide, the total area is about 450 ha, and it is composed of natural and man-  
123 made water bodies with sand dunes separating the water bays of the lakes.

124 To study incubation behavior and manipulate the thermal condition of the nest an  
125 automatic nest monitoring system was developed (Figure 1). The system consisted of  
126 four main parts. First, an electronic balance (Navigator, Ohaus Corporation, Pine Brook,  
127 New Jersey, USA) was placed under the nest scrape and connected to a data logger  
128 (Gigalog, Audon Electronics, Nottingham, UK) to record the body mass of the  
129 incubating parent every 20 s. The nest was placed on a plastic tray on top of the balance.  
130 The extreme ambient temperature (see below) and strong wind, however, made the  
131 readings of the balance unreliable, so these measurements were not investigated further.  
132 Second, a thermo-probe was inserted into the bottom of the nest scrape, and another  
133 probe about 25 cm from the nest scrape at ground level to measure the thermal  
134 condition of the nest and the environment, respectively. The probes were connected to a  
135 data logger (Tinytag, Gemini Data Loggers Ltd., Chichester, UK) that recorded data  
136 every 20 s. Third, a small spy camera (Outdoorcam, Swann Communications Pty. Ltd.,  
137 Richmond, Victoria, Australia) was positioned about 1 m from the nest and connected  
138 to a digital video recorder (MemoCam, Video Domain Technologies Ltd., Petah Tikva,  
139 Israel) to record the behavior of the parents every 20 s. The camera had infrared light

140 sources that allowed recording of behavior at night. The plumage of adult Kentish  
141 plovers is sexually dimorphic during the breeding season and this allows identification  
142 of sexes from the photos. Fourth, a Peltier heat pump (RS Components Ltd., Corby,  
143 UK) was placed under the nest scrape to change the thermal condition of the nest. This  
144 device was connected to a central unit that was remote controlled. The power was  
145 supplied by a car battery. All parts of the system (except the camera) and the cables  
146 were hidden underground to minimize the disturbance to the plovers.

147       The experiment lasted for four days at each nest. Before the experiment both  
148 parents were captured, measured and color ringed. All experimental nests had three  
149 eggs (modal clutch size), and the clutches were  $11.9 \pm 1.02$  (mean  $\pm$  SE,  $n = 20$ ) days  
150 old at the start of the experiment. On the first day the system was set up at the nest, the  
151 second day was a baseline, and on the third and fourth days we cooled the nest between  
152 either 22:00 – 04:00 or 05:00 – 09:00 to target the male or female, respectively (Figure  
153 2). The order of cooling was randomized at a nest. The system was visited daily to  
154 change memory cards in data loggers, to change the battery (every 2nd day), and to  
155 check the system for proper operation. The mean length of these visits were  $20.1 \pm 0.56$   
156 min (mean  $\pm$  SE,  $n = 20$ ), and data from these periods were excluded from the analyses.  
157 No visit was made during the manipulations (i.e. during cooling).

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

163       We expected that the parents aim to mitigate the effect of cooling on egg



164 temperatures. To assess the effect of cooling on nest temperature without the parents,  
165 we measured nest and ambient temperatures at five unused nests ('dummy nests'  
166 henceforward; three nests in 2005 and two in 2006). In these cases the nest monitoring  
167 system was set up at previously predated, abandoned or hatched Kentish plover nests  
168 for one day, and three fresh eggs of Japanese quail *Coturnix japonica* were cooled for  
169 equivalent periods for the male and female manipulation (22:00 – 04:00 or 05:00 –  
170 09:00, respectively). The quail egg is similar in size and shape to the Kentish plover  
171 egg.

## 172 **Statistical analyses**

173 We considered each nest as the unit of analysis. The effect of manipulation on  
174 incubation behavior was measured by the change in incubation time (%; i.e. percentage  
175 of incubation during manipulation day minus percentage of incubation during baseline  
176 day). The baseline and manipulation days were divided into two parts: manipulation  
177 period (22:00 – 04:00 and 05:00 – 09:00 for male and female manipulation day,  
178 respectively), and after manipulation period (04:00 – 10:00 and 09:00 – 13:00 for male  
179 and female manipulation day, respectively). The responses by the male and female  
180 during and after manipulation were not influenced significantly by year, by the nest  
181 monitoring system (set one or set two) used for data collection and manipulation, or by  
182 the order of manipulation (ANOVAs,  $p \geq 0.194$  in all cases), therefore these effects  
183 were not considered in further analyses.

184       With the 22:00 – 04:00 manipulation period we targeted the male, whereas with the  
185 05:00 – 09:00 period the female parent was targeted. However, the targeted parent did  
186 not always incubate during the whole cooling period (see below); thus the amount of

187 manipulation experienced by a given parent depended on the time it spent on the nest  
188 during manipulation. Therefore, we used a covariate ( $\Delta T$ ) in the linear models to  
189 investigate the effect of manipulation on the response of the sexes.  $\Delta T$  for a given sex  
190 was defined as the absolute value of the effect of cooling on nest temperature ( $T_{nest}$ -  
191  $T_{ambient}$ ) multiplied by the time the parent was incubating the nest during the cooling  
192 period. The effect of cooling for a given day of the season was estimated by using the  
193 temperature data of dummy nests (see below).

194 The presence of parents influenced the effect of cooling because the difference  
195 between nest and ambient temperature ( $T_{nest}-T_{ambient}$ ) was smaller at experimental nests  
196 than at dummy nests (22:00 – 04:00, experimental nests:  $-1.2 \pm 0.27$  °C, dummy nests: -  
197  $4.2 \pm 0.52$  °C; t-test,  $t_{23} = 4.924$ ,  $p < 0.001$ ; 05:00 – 09:00, experimental nests: -  
198  $3.3 \pm 0.25$  °C, dummy nests:  $-5.9 \pm 0.32$  °C;  $t_{20} = 5.245$ ,  $p < 0.001$ ). Furthermore, the  
199 effect of cooling (i.e.  $T_{nest}-T_{ambient}$ ) at dummy nests tended to be larger in absolute value  
200 over the breeding season (least-squares regressions, male manipulation:  $B = -$   
201  $0.02 \pm 0.021$ ;  $t_3 = 1.157$ ,  $p = 0.331$ ; female manipulation:  $B = -0.02 \pm 0.007$ ;  $t_3 = 3.552$ ,  
202  $p = 0.038$ ). Therefore, the manipulations received by the sexes ( $\Delta Ts$ ) were estimated  
203 using temperature difference ( $T_{nest}-T_{ambient}$ ) estimated for a given date using the  
204 coefficients of the above least-squares regressions.

205 During male-targeted manipulations the male was on the nest  $70.2 \pm 5.06\%$  of the  
206 time (mean  $\pm$  SE), the female  $26.2 \pm 4.71\%$ , and neither parent  $3.6 \pm 0.71\%$ . That is,  
207 males spent more time on the nest than females when males were targeted (paired t-test,  
208  $t_{19} = 4.522$ ,  $p < 0.001$ ). In contrast, during female-targeted manipulations the females  
209 spent more time on the nest than males ( $t_{16} = 11.525$ ,  $p < 0.001$ ; male:  $9.1 \pm 2.84\%$ ,  
210 female:  $77.3 \pm 3.41\%$ , neither:  $13.6 \pm 2.10\%$ ). Thus, during male-targeted manipulations

211 the males experienced more cooling than females ( $\Delta T_{male} = 17.5 \pm 1.34 \text{ }^\circ\text{C} \times \text{h}$ ,  
212  $\Delta T_{female} = 6.8 \pm 1.28 \text{ }^\circ\text{C} \times \text{h}$ ; paired t-test,  $t_{19} = 4.321$ ,  $p < 0.001$ ), whereas during female-  
213 targeted manipulations females experienced more cooling than males  
214 ( $\Delta T_{male} = 2.1 \pm 0.69 \text{ }^\circ\text{C} \times \text{h}$ ,  $\Delta T_{female} = 18.2 \pm 0.94 \text{ }^\circ\text{C} \times \text{h}$ ;  $t_{16} = 10.694$ ,  $p < 0.001$ ). This  
215 is, of course, what the experiment was designed to achieve, but we stress that ‘male’  
216 and ‘female’ targeting was a statistical, not deterministic, difference because sometimes  
217 the ‘wrong’ sex was present and experienced the manipulation targeted at its mate.

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

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

232 To investigate the distribution of vectors, we divided the parameter space into two  
233 triangles along the male change = female change (+1 slope) line (isocline,  
234 henceforward). Vectors between  $0^\circ$  and  $45^\circ$  either side of the isocline mean that both

235 parents increased incubation ('matching', see Figure 3), vectors between 45° and 135°  
236 mean that one parent increased incubation while the other decreased ('compensation' by  
237 the female or the male; upper left and lower right triangles, respectively), whereas  
238 vectors between 135° and 180° mean that both parents decreased incubation ('negative  
239 matching').

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

247 Statistical analyses were carried out using R 2.6.0 (R Development Core Team  
248 2007). Values are given as mean  $\pm$  SE unless indicated otherwise.

## 249 **Results**

### 250 **Effect of manipulation on incubation behavior**

251 Cooling of the eggs influenced parental behavior: total incubation was higher during  
252 male manipulation than during baseline periods, and total incubation increased with the  
253 cooling the parents experienced (Table 1). Males, but not females, increased their  
254 incubation time with the manipulation they received (regression on  $\Delta T$ ). After  
255 manipulation, male incubation non-significantly tended to decrease, whereas female  
256 incubation increased compared to the baseline day (Table 1). Similar to the preceding

257 results, total incubation was higher during female manipulation than during baseline  
258 (Table 1). Furthermore, incubation by females, but not males, was higher during the  
259 manipulation than baseline (Table 1). After female manipulation, total incubation was  
260 significantly higher in nests that had previously received more cooling (regression on  
261  $\Delta T$ ), but no other relationships after female manipulation were significant (Table 1).  
262 The non-significant trend was for females to decrease incubation, and for males to  
263 increase, after female manipulation.

264       Whilst these results show that the manipulation had an effect on parental behavior,  
265 they cannot explain how a parent responded to the changed effort of its mate, because  
266 here males and females were tested independently. Furthermore, the slopes on  $\Delta T$  are  
267 not comparable between the sexes because the ranges of the explanatory variable (i.e.  
268 the amount of manipulation received) were different between males and females (see  
269 Methods for the mean  $\Delta T$  received by the sexes).

## 270 **Response to mate's behavior**

271 Compensation by the mate, rather than matching, was the most common response to the  
272 manipulation. Firstly, during male manipulations the mean angle of vectors from the  
273 isocline and their 95% confidence interval fell into the compensation area (mean: 68.3°,  
274 95% CI: 57.0° – 79.6°,  $n = 19$ ). Similarly, the mean vectors and their confidence areas  
275 were restricted (upper left triangle) or almost restricted (lower right triangle) to the  
276 compensation areas (Figure 3). Unexpectedly, in nine out of 19 nests, the female  
277 increased her incubation (and the male showed compensatory decrease) when the male  
278 was the intended target. We investigated why this might have happened. It turned out  
279 that at these nine nests the females experienced significantly more cooling

280  $(\Delta T_{prop} = \Delta T_{female} \times (\Delta T_{male} + \Delta T_{female})^{-1} = 0.41 \pm 0.060)$ , than at the other ten nests  
281  $(\Delta T_{prop} = 0.18 \pm 0.063; t\text{-test}, t_{17} = 2.579, p = 0.019)$ .

282 Secondly, the effects of female manipulations were consistent with that of the male  
283 manipulations (mean angle:  $70.2^\circ$ , 95% CI:  $56.8^\circ - 83.7^\circ$ ,  $n = 17$ ), and the mean vectors  
284 and their confidence areas were nearly always in the compensation areas (Figure 3).

285 Thirdly, after manipulations the responses of the parents with respect to each other  
286 were similar to the ones during manipulations, because the mean angle of vectors were  
287 inside the compensation areas (male manipulation, mean:  $85.7^\circ$ , 95% CI:  $64.9^\circ - 106.5^\circ$ ,  
288  $n = 20$ ; female manipulation, mean:  $90.4^\circ$ , 95% CI:  $76.9^\circ - 103.9^\circ$ ,  $n = 17$ ).

289 Furthermore, both the mean vectors and their confidence areas were largely restricted to  
290 the compensation areas (Figure 3).

291 It is unlikely that the compensatory responses were due to an upper limit in total  
292 incubation, because the percentage of time the two parents spent on the nest was  
293 significantly different from 100% during the manipulation and after manipulation  
294 periods on both manipulation days (during male manipulation:  $96.4 \pm 0.71\%$ ,  
295  $t_{19} = 5.052, p < 0.001$ ; after male manipulation:  $85.5 \pm 1.68\%$ ,  $t_{19} = 8.626, p < 0.001$ ;  
296 during female manipulation:  $86.4 \pm 2.10\%$ ,  $t_{16} = 6.471, p < 0.001$ ; after female  
297 manipulation:  $94.0 \pm 1.99\%$ ,  $t_{16} = 3.039, p = 0.008$ , see also Methods for a summary of  
298 ceiling effect analyses).

### 299 **Consistency of responses**

300 Finally, the responses of parents were highly consistent between male and female  
301 manipulations (Figure 4,  $n = 13$  pairs out of 16 were in, or on the border of, the  
302 compensation area, i.e. within 25% of the whole parameter space; binomial test using

303  $P = 0.25$ ,  $p < 0.001$ ), and after manipulations ( $n = 11$  pairs out of 17;  $p = 0.001$ ).

## 304 **Discussion**

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

315       Second, we showed that compensation, rather than matching, was the most  
316 common response by Kentish plover parents to cooling of the eggs (or the partner’s  
317 response to cooling). That is, our results are in line with theoretical models that predict  
318 compensation between parents (McNamara et al. 1999, Johnstone & Hinde 2006).  
319 Unlike most previous experimental manipulations of parental effort, our manipulations  
320 aimed at increasing the contribution of the targeted parents (*cf.* handicapping and  
321 removal), and we did achieve this because total incubation increased during both  
322 manipulation periods compared to the baseline day. When one parent increased its  
323 incubation time in response to egg cooling, the response of the partner was usually not  
324 to keep its own effort constant, or match it, but to decrease it. The latter result suggests  
325 that there is a conflict between the parents over the amount of parental effort, and that

326 each parent tries to avoid the costs of parental care and shunt the work on its partner  
327 (Houston et al. 2005). Some of our results indicate overcompensation (e.g. increasing  
328 total incubation). These results are intriguing because they are not in line with the  
329 results of most previous experiments and the predictions of theoretical models.  
330 However, our results are not comparable to previous studies because we aimed at  
331 increasing the effort of the manipulated parents.

332 Third, the parents' responses were consistent during the manipulation and after  
333 manipulation periods, since most pairs exhibited compensation during all four periods.  
334 This consistency strengthens the suggestion that the actual changes in parental effort are  
335 results of a negotiation process.

336 To our knowledge, the only experimental study on parental effort that, similarly to  
337 our study, has aimed at increasing the contribution of the targeted parent was Hinde  
338 (2006). Using playback of begging calls to modulate feeding rates in great tit, she  
339 showed matching rather than compensation between parents. The reason for these  
340 contrasting results may lie in the differences in information available for the parents,  
341 since the information the parents have on the need or value of offspring may profoundly  
342 influence whether compensation or matching is the outcome of the negotiation process  
343 (Johnstone & Hinde 2006). Our results are in line with the predictions of Johnstone &  
344 Hinde (2006), because compensation is expected if the parents have reliable and  
345 symmetric information about the need of the offspring, which in the Kentish plover may  
346 be the difference between the optimal and actual egg temperature. In contrast, in Hinde  
347 (2006) the great tit parents may have used the mate's increased work rate as a cue of  
348 increased brood need or quality, and they responded by matching, as predicted by  
349 Johnstone & Hinde (2006) if the parents have only partial information regarding brood



350 need and quality.

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

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

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371

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## 379 **References**

- 380 Alatalo RV, Gottlander K, Lundberg A. 1988. Conflict or cooperation between parents  
381 in feeding nestlings in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scand.*  
382 19:31–34.
- 383 Amat JA, Fraga RM, Arroyo GM. 1999. Brood desertion and polygamous breeding in  
384 the Kentish plover *Charadrius alexandrinus*. *Ibis*. 141:596–607.
- 385 Balshine S, Kempenaers B, Székely T. 2002. Conflict and cooperation in parental care –  
386 Introduction. *Phil Trans R Soc Lond B*. 357:237–240.
- 387 Bart J, Tornes A. 1989. Importance of monogamous male birds in determining  
388 reproductive success. *Behav Ecol and Sociobiol*. 24:109-116.
- 389 Clutton-Brock TH. 1991. *The Evolution of Parental Care*. Princeton: Princeton  
390 University Press.
- 391 Erckmann WJ. 1983. The evolution of polyandry in shorebirds: An evaluation of  
392 hypotheses, In: Wasser SK, editor. *Social Behavior of Female Vertebrates*. New  
393 York: Academic Press. p. 113–168.
- 394 Fraga RM, Amat JA. 1996. Breeding biology of a Kentish plover (*Charadrius*  
395 *alexandrinus*) population in an inland saline lake. *Ardeola*. 43:69–85.

- 396 Hinde CA. 2006. Negotiation over offspring care? A positive response to partner-  
397 provisioning rate in great tits. *Behav Ecol.* 17:6–12.
- 398 Houston AI, Davies NB. 1985. The evolution of cooperation and life history in the  
399 dunnock, *Prunella modularis*. In: Sibly RM, Smith RH, editors. *Behavioural*  
400 *ecology: ecological consequences of adaptive behaviour*. Oxford: Blackwell  
401 Scientific Publications. p. 471–487.
- 402 Houston AI, Székely T, McNamara JM. 2005. Conflict over parental care. *Trends Ecol*  
403 *Evol.* 20:33–38.
- 404 Johnstone RA, Hinde CA. 2006. Negotiation over offspring care – how should parents  
405 respond to each other’s efforts? *Behav Ecol.* 17:818–827.
- 406 Kosztolányi A, Székely T. 2002. Using a transponder system to monitor incubation  
407 routines of snowy plovers. *J Field Ornith.* 73:199–205.
- 408 Kosztolányi A, Székely T, Cuthill IC, Yılmaz KT, Berberoğlu S. 2006. Ecological  
409 constraints on breeding system evolution: the influence of habitat on brood  
410 desertion in Kentish plover. *J Anim Ecol.* 75:257–265.
- 411 Lessells CM. 1984. The mating system of Kentish plovers *Charadrius alexandrinus*.  
412 *Ibis.* 126:474–483.
- 413 Lessells CM. 1999. Sexual conflict in animals. In: Keller L, editor. *Levels of Selection*  
414 *in Evolution*. Princeton: Princeton University Press. p. 75–99.
- 415 Markman S, Yom-Tov Y, Wright J. 1995. Male parental care in the orange-tufted  
416 sunbird: behavioural adjustments in provisioning and nest guarding effort. *Anim*  
417 *Behav.* 50:655–669.
- 418 Markman S, Yom-Tov Y, Wright J. 1996. The effect of male removal on female  
419 parental care in the orange-tufted sunbird. *Anim Behav.* 52:437–444.

- 420 Martin K, Cooke F. 1987. Bi-parental care in willow ptarmigan: a luxury? *Anim Behav.*  
421 35:369–379.
- 422 McNamara JM, Gasson CE, Houston AI. 1999. Incorporating rules for responding into  
423 evolutionary games. *Nature.* 401:368–371.
- 424 Olson VA, Liker A, Freckleton RP, Székely T. 2008. Parental conflict in birds:  
425 comparative analyses of offspring development, ecology and mating  
426 opportunities. *Proc Roy Soc B.* 275:301–307.
- 427 Parker G, Royle NJ, Hartley IR. 2002. Intrafamilial conflict and parental investment: a  
428 synthesis. *Phil Trans R Soc B.* 357:295–307.
- 429 Rittinghaus H. 1961. *Der Seeregenpfeifer(Charadrius alexandrinus L.)*. Wittenberg,  
430 Lutherstadt: A. Ziemsen Verlag.
- 431 Sanz JJ, Kranenbarg S, Tinbergen JM. 2000. Differential response by males and  
432 females to manipulation of partner contribution in the great tit (*Parus major*). *J*  
433 *Anim Ecol.* 69:74–84.
- 434 Schwagmeyer P, Mock DW, Parker GA. 2002. Biparental care in house sparrows:  
435 negotiation or sealed bid? *Behav Ecol.* 13:713–721.
- 436 Slagsvold T, Lifjeld JT. 1990. Influence of male and female quality on clutch size in tits  
437 (*Parus spp.*). *Ecology.* 71:1258–1266.
- 438 Smiseth PT, Amundsen T. 2000. Does female plumage coloration signal parental  
439 quality? A male removal experiment with the bluethroat (*Luscinia s. svecica*).  
440 *Behav Ecol and Sociobiol.* 47:205–212.
- 441 Smiseth PT, Dawson C, Varley E, Moore AJ. 2005. How do caring parents respond to  
442 mate loss? Differential response by males and females. *Anim Behav.* 69:551–559.
- 443 Taylor PD, Day T. 2004. Stability in negotiation games and the emergence of

444 cooperation. *Proc Roy Soc B*. 271:669–674.

445 Thomas GH, Székely T, Reynolds JD. 2007. Sexual conflict and the evolution of  
446 breeding systems in shorebirds. *Adv Study Behav*. 37:279–342.

447 Trivers R. 1972. Parental investment and sexual selection. In: Campbell B, editor.  
448 Sexual Selection and the Descent of Man. Chicago: Aldine Press. p. 136–179.

449 Warriner JS, Warriner JC, Page GW, Stenzel LE. 1986. Mating system and reproductive  
450 success of a small population of polygamous snowy plovers. *Wilson Bull*. 98:15–  
451 37.

452 Wright J, Cuthill IC. 1989. Manipulation of sex differences in parental care. *Behav Ecol*  
453 and *Sociobiol*. 25:171–181.

454

455 **Figure legends**

456 **Figure 1**

457 The system we used for monitoring and manipulating nest temperatures in the field. (a)  
458 The camera with a Kentish plover nest, (b) the electronic balance, datalogger and  
459 Tinytag temperature logger, (c) the video recorder, the main unit (controlling the Peltier  
460 device and distributing power), and the battery in a separate box about 5 m from the  
461 nest.

462

463 **Figure 2**

464 The effects of cooling on internal nest temperature (solid line) and the ambient ground  
465 temperature (broken line) at an experimental nest. In this example the first cooling  
466 targeted the male, and the second cooling the female.

467

468 **Figure 3**

469 The responses of Kentish plover parents during manipulation (left panels) and after  
470 manipulation (right panels). The thick vectors are the mean of vectors in the upper left  
471 and lower right triangles, and the shaded boxes are the 95% confidence areas for the  
472 mean vectors. The number of nests ( $n$ ) is given for each triangle (see Methods).

473

474 **Figure 4**

475 Summary of parental responses. Angles are given as the absolute deviation from the  
476 isocline (see Methods). The behaviors of a pair during manipulation (●) and after  
477 manipulation (○) are connected.

478 **Table 1**

479 Change in incubation time (% , manipulation – baseline) in Kentish plover parents, and  
 480 the effect of received manipulation ( $\Delta T$ , °C × h) on the change in incubation time  
 481 expressed as the slope of least-squares regressions.  $\Delta T_{sex}$  means manipulation received  
 482 by the male, the female and by both sexes, respectively.

**Male manipulation**

**During manipulation (22:00 – 04:00)**

	<b>Change in incubation</b>	<b>Slope on <math>\Delta T_{sex}</math></b>
Male	3.3 ± 4.80, $p = 0.498$	<b>1.9 ± 0.71, <math>p = 0.014</math></b>
Female	1.9 ± 4.36, $p = 0.671$	1.3 ± 0.74, $p = 0.104$
Total	<b>5.2 ± 1.79, <math>p = 0.009</math></b>	<b>1.1 ± 0.43, <math>p = 0.026</math></b>

**After manipulation (04:00 – 10:00)**

Male	-5.1 ± 2.66, $p = 0.070$	0.5 ± 0.46, $p = 0.317$
Female	<b>11.4 ± 4.09, <math>p = 0.011</math></b>	-1.1 ± 0.70, $p = 0.126$
Total	6.3 ± 3.67, $p = 0.100$	0.4 ± 1.02, $p = 0.731$

**Female manipulation**

**During manipulation (05:00 – 09:00)**

Male	-4.0 ± 2.49, $p = 0.131$	-0.3 ± 0.93, $p = 0.723$
Female	<b>19.3 ± 6.42, <math>p = 0.008</math></b>	2.6 ± 1.62, $p = 0.122$
Total	<b>15.4 ± 5.74, <math>p = 0.017</math></b>	3.5 ± 1.94, $p = 0.093$

**After manipulation (09:00 – 13:00)**

Male	0.6 ± 3.42, $p = 0.859$	-0.8 ± 1.26, $p = 0.514$
Female	-1.7 ± 3.06, $p = 0.584$	-0.4 ± 0.83, $p = 0.613$
Total	-1.1 ± 1.50, $p = 0.475$	<b>1.1 ± 0.48, <math>p = 0.037</math></b>

483

484 Means ± SEs, and probabilities from one-sample t-tests on the change in incubation  
 485 ( $df = 19$  and  $df = 16$  for male and female manipulation, respectively), and on the slope  
 486 of least-squares regressions ( $df = 18$  and  $df = 15$  for male and female manipulation,  
 487 respectively) are given. Statistically significant values are in bold.