



Body mass dynamics during incubation and duration of parental care in Pacific Dunlins *Calidris alpina pacifica*: a test of the differential parental capacity hypothesis

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Breeding is energetically expensive and individuals face a trade-off between current and future breeding investment. Due to their production of large eggs, female birds are thought to have substantially higher initial energetic investments than males, which decrease the female's offspring rearing capacity. The differential parental capacity hypothesis argues that this large initial investment limits the ability of female shorebirds to provide extended parental care, which can ultimately lead to offspring desertion. This hypothesis predicts that (1) during early incubation females will be in poorer condition than males, (2) both sexes will lose condition during incubation, but the decline in females will be slower than the decline in males and (3) there will be a positive relationship between female condition and the duration of maternal brood care. These predictions were tested using data on body mass adjusted for body size (as a proxy for condition) and parental care from Pacific Dunlins *Calidris alpina pacifica* nesting on the Yukon Kuskokwim Delta, Alaska. None of the predictions received support: females were heavier than males in early incubation, the overall pattern during incubation was that males gained mass while female mass remained relatively constant, and there was no relationship between female mass and maternal brood care duration. These results suggest that the factors influencing parental care decisions are more complex than a parent simply caring until it is physiologically unable to do so.

Keywords: breeding investment, brood desertion, negotiation, shorebird, wader.

Parental care is any behaviour of an individual that is directed towards its offspring in order to enhance the offspring's fitness (Clutton-Brock 1991). It can be a costly behaviour when the time and energy an individual invests in its current offspring comes at a cost to future reproduction (Williams 1966). This cost results in sexual conflict because an individual

should prefer that their mate increases their investment while they limit their own (Trivers 1972, Houston *et al.* 2005).

Naturally, parental care is not the only investment in reproduction; gamete formation can also entail substantial energetic expenditure. This pre-fertilization investment is not equal between sexes, with females usually investing more heavily in gamete production (Hayward & Gillooly 2011), followed by an additional large investment by the female whereby she provides for the developing embryo/foetus (Gittleman & Thompson 1988, Vézina & Williams 2005). In most circumstances, unlike incubation and offspring care, males are unable to contribute directly to this investment.

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There are many examples that demonstrate the high cost of egg production in birds (reviewed in Nager 2006). For instance, clutch-size manipulation experiments that induce females to lay larger than normal clutches have revealed that the production of additional eggs can have negative ramifications both in the short term (e.g. poor fledgling success, Monaghan *et al.* 1998) and the long term (e.g. smaller clutch size the following season, Bowers *et al.* 2012). It has been hypothesized that this large initial energetic investment by the female bird can also limit her ability to provide extended parental care (Maynard Smith 1977, Nager 2006). Based on the large investment of females into egg production, Erckmann (1983) proposed the differential parental capacity hypothesis (henceforth DPCH) to explain why female brood desertion is a relatively common behaviour in sandpipers (Scolopacidae). He suggested that brood desertion by female sandpipers is due to their poor body condition relative to that of their mates. More specifically, he proposed that a female deserts because she has the high energy investment of egg production early in the season and her costs of breeding continue to mount through incubation until her body condition declines to a point where continuing to care would limit her ability to breed in the future, and as a result she deserts her current brood (Erckmann 1983, Amat *et al.* 2000). By deserting, a female sandpiper should be able to devote more time to foraging, thus regaining her body condition sooner than if she had remained with the brood, consequently increasing her probability of surviving until the next season.

I investigated the DPCH by examining the body mass dynamics and duration of parental care of Pacific Dunlins *Calidris alpina pacifica*. Specifically, I tested the following three predictions. First, due to the females' heavy investment during egg production, they will be in poorer condition in early incubation than males (Erckmann 1983). Secondly, incubation is energetically costly (Williams 1996); thus I predicted that both males and females will lose condition during incubation. However, as females have already invested heavily, they should be more prudent with their remaining reserves. As a result, females should have a lower rate of change than males because if females were to lose condition too rapidly during incubation, they would risk reaching their desertion threshold during incubation, and sustain a high fitness cost.

Thirdly, if a female's condition dictates how much brood care she is able to provide, females in better condition at the end of incubation should have longer brood care duration than females in poorer condition because they will have more endogenous energy reserves to invest during this period (Amat *et al.* 2000).

The Dunlin is a suitable species to test the above predictions as they exhibit bi-parental incubation and male-biased brood care. Compared with species in which the males do not assist with parental care, the fitness cost to the females for deserting her brood should be relatively low. This should enable females to invest amply in egg production, even at the expense of relatively poor body condition. Furthermore, the exact timing of brood desertion varies greatly between females within the same population (0–12 days after hatching; Jamieson 2011), which gives a readily measurable characteristic of female parental investment. Amat *et al.* (2000) tested the DPCH, and found little support for it, using data collected on Kentish Plovers *Charadrius alexandrinus* in Spain. However, incubation costs rise with latitude (Piersma *et al.* 2003) and thus the cost of incubation in that population of Kentish Plovers was likely to be relatively low. It might be better to test the hypothesis using a species that breeds in the sub-Arctic, such as the Dunlin, where the elevated cost of incubation and thermoregulation will be more likely to push the female towards the desertion threshold. Indeed, female sub-Arctic Dunlins desert their broods at a higher frequency (95%, Jamieson 2011) than female Kentish Plovers in Spain (84%, Amat *et al.* 1999).

METHODS

The breeding ecology of Dunlins was studied near Kanaryarmiut Field Station, Yukon Delta National Wildlife Refuge, Yukon Kuskokwim Delta, Alaska (61°22'N, 165°07'W) during the summers of 2005 and 2006. Dunlins lay a four-egg clutch that is incubated by both parents for approximately 22 days (Holmes 1966, Jamieson 2011). Females usually desert the brood shortly after hatching (mean = 5.0 days, 95% confidence limits = 3.9–6.1 days, $n = 60$), while the males remain with the chicks until they fledge (~ 19 days); however, in 5% of Dunlin pairs studied on the Yukon Kuskokwim Delta it was the male that deserted first, leaving the care to the female (Jamieson

2011). Dunlins are capable of double-brooding; i.e. after deserting their first brood, individuals pair with new mates and produce second clutches (Soikkeli 1967, Jamieson 2011). Brood care involves brooding, leading the chicks to feeding areas, protecting them from predators and keeping the brood together.

Dunlins nested in graminoid-dominated lowland wet meadows interlaced with small ponds and rivers. Nests were found through behavioural observations and territory mapping. The study site was surveyed every 1–3 days and all individual Dunlins observed were noted. All nesting territories defended by males were plotted and systematically searched for nests. Each nest was visited daily until the clutch was complete (i.e. four eggs or the same number of eggs for three consecutive days). The date the last egg was laid was defined as day zero of the incubation period (referred to as 'incubation date'). However, many of the nests were found complete (57%) so the flotation method was used to estimate their incubation dates (Liebezeit *et al.* 2007). If the eggs floated at an angle of 90°, the nest was examined every 3 days for signs of hatching and the incubation date was back-calculated from the observed hatching date (incubation length assumed to be 22 days).

Each incubating bird was captured using a bow-net and marked with a unique combination of three coloured darvic bands (mean day of incubation at time of ringing = 5.5, 95% confidence limits = 4.7–6.3, $n = 90$). Tarsus-length (to a precision of 0.1 mm), culmen-length (to 0.1 mm), wing chord-length (to 1 mm) and body mass (to 0.1 g) were measured and recorded. The sex of each adult was determined by culmen-length (females ≥ 39.8 mm, males ≤ 37.7 mm; Page 1974). There were two males and 10 females whose culmen lengths fell inside the overlap range (i.e. 37.8–39.7 mm); fortunately they were mated with individuals whose culmen lengths fell into a definitive sex category, so they were classified as the opposite sex. There were no cases where the sex classification as determined by culmen length (or their mate's culmen length) conflicted with observed mating behaviours or vocalizations. Approximately 10 days after their first trapping, birds were retrapped and reweighed. After the second visit, rate of change in body mass per day (Δ body mass, g/day) was estimated for each individual by calculating the difference in body mass between successive measurements divided by

the number of days that lapsed between visits. There were nine occasions where the nest hatched or failed before both parents were trapped for the second time.

Nests were checked every 1–3 days for incubation activity. After hatching, broods were visited daily and the identity of the attending parent(s) was recorded. Determining the exact number of chicks present was not usually possible due to their secretive behaviour and the tall vegetation. A parent was considered to have deserted if it was not observed with its brood for three consecutive days and the date of desertion was deemed to be the day after the parent was last seen. Of the 28 families followed to determine the timing of female desertion, there were no instances where the female reappeared after the family was classified as deserted.

Statistical analysis

Thirty-seven males and 38 females from 43 breeding attempts were trapped and measured twice during incubation (2005: ♂ = 17, ♀ = 19; 2006: ♂ = 20, ♀ = 19) and these data were used to test the first and second predictions. These numbers include data from both members of 32 pairs and 11 individuals whose partner was not caught. Pairs were targeted because both members were likely to use the same foraging habitat and thus limit any influence that habitat quality might have in the analysis. An additional seven males and eight females were captured and weighed once during early incubation before their nests failed (2005: ♂ = 1, ♀ = 2; 2006: ♂ = 6, ♀ = 6) and were added to the dataset to test Prediction 1. Body mass during late incubation and parental care duration data were collected for 28 females (2005: 13; 2006: 15); these data were used to test the third prediction (10 of the females weighed twice during incubation had their nests or broods depredated prior to female brood desertion).

Backwards stepwise regressions were used to test the predictions. At each step the variable with the highest P -value was removed from the analysis and the regression was rerun. This process was repeated until only those variables that contributed significantly to explaining variation in the dependent variables remained ($P < 0.05$). The dependent variables were body mass during early incubation, Δ body mass and female parental care duration for Predictions 1, 2 and 3, respectively.

The independent factors of interest were sex for the first and second predictions and female body mass during late incubation (between days 10 and 20 of incubation) for the third. Year was included as a factor in all models. For each analysis, first principal component scores (PC1) were calculated using a principal component analysis with a correlation matrix of tarsus length, culmen length, and wing chord length and PC1 was then included as a covariate to control for differences in body size (Freckleton 2002, Krapu *et al.* 2006). PC1 explained 45% of the total observed variance. Day of incubation and day of the year that body mass was measured were included as covariates in the analyses testing Predictions 1 and 3 and day of incubation of the final body mass measurement was included in the analyses testing Prediction 2 to control for any effects of data collection timing. The amount of care provided by the female varies with date (Jamieson 2011) and parental body mass can decline rapidly at the time of hatching (Tulp *et al.* 2002). Body mass can also vary diurnally (Szentirmai *et al.* 2001). Although the exact time of data collection was not systematically recorded in my study, the data were collected at random times throughout the day.

I used body mass adjusted for body size as a proxy for condition (see Jamieson *et al.* 2006), as no alternative non-invasive measure of body condition was available. All data are reported as means \pm 95% confidence intervals. In all tests, statistical significance was accepted at $\alpha = 0.05$. Analyses were carried out using SYSTAT 12 (Systat Software Inc., Chicago, IL, USA).

RESULTS

There was a significant sex difference in early incubation body mass but not in the direction predicted. Females were heavier than males (Prediction 1; sex: $F_{1,88} = 75.30$, $P = 0.005$ when controlling for body size (PC1): $F_{1,88} = 112.87$, $P = 0.001$; Fig. 1). The remaining variables were removed from the model as they did not contribute significantly to explaining the variation observed in body mass (all $P > 0.05$).

There was a significant sex difference in body mass dynamics during incubation (Prediction 2; sex: $F_{1,73} = 7.34$, $P = 0.008$; Fig. 2). The prediction was that females would lose body mass more slowly than males but, on average, males gained body mass during incubation ($+0.12 \pm 0.09$ g/day;

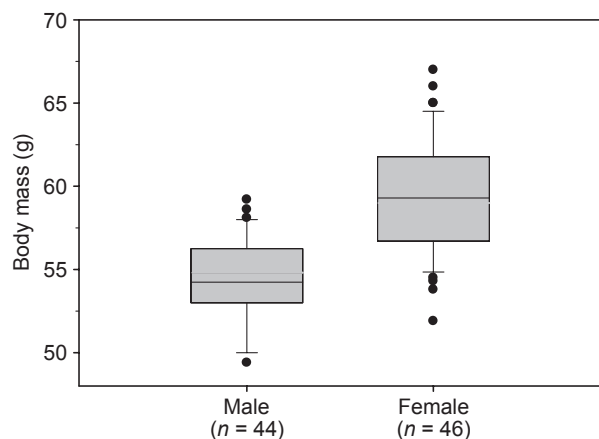


Figure 1. During early incubation, female Dunlins breeding on the Yukon Kuskokwim Delta, Alaska, were significantly heavier than their male counterparts ($P < 0.005$). Whiskers signify 90th and 10th percentiles, the outer edges of the box represent the 25th and 75th percentiles, the solid line in the box is the mean and trailing dots are outliers.

$n = 37$), whereas females remained relatively constant (-0.05 ± 0.09 g/day; $n = 38$). No other variable contributed significantly to the model (all $P > 0.05$).

The third prediction, that females that were heavier during late incubation would remain with their broods longer, was also unsupported. On average, females provided 6.9 ± 1.8 days of brood care (range: 0–19 days; $n = 28$) and body mass did not have a significant effect on female brood care duration ($F_{1,23} = 0.079$, $P > 0.05$; Fig. 3), nor did any other variable (all $P > 0.05$).

DISCUSSION

I found no support for the hypothesis that the sex-specific parental care patterns observed in Dunlins were associated with differences between the sexes in their energetic investment in early reproduction. Even after adjusting for differences in body size with PC1, females were in better condition than males in early incubation. Moreover, during incubation, males gained mass while females maintained their body mass; taken at face value, this suggests that females were investing more energy than males. Finally, there was no significant relationship between the amount of time a female remained with her brood before deserting it and her body mass during late incubation. My results agree with those of Amat *et al.* (2000), who also

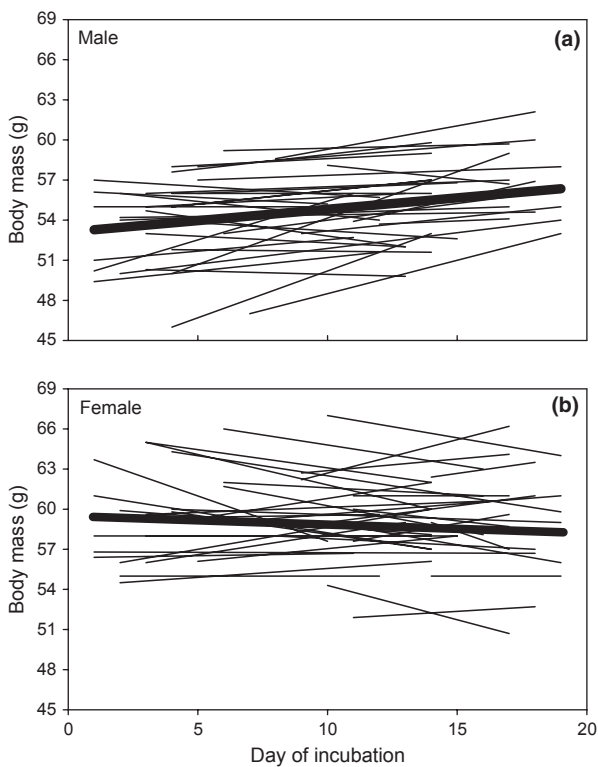


Figure 2. Raw data of body mass changes in Dunlins nesting on the Yukon Kuskokwim Delta, Alaska. There were significant differences in how body mass changed between the sexes ($P = 0.008$); male Dunlins gained body mass, whereas females' mass remained stable (♂ one-sample t -test, $t = 2.73$, $df = 36$, $P = 0.009$; ♀ one-sample t -test, $t = 0.29$, $df = 37$, $P = 0.292$). The endpoints of each line represent the two sets of data collected for each bird and are connected by a straight line. The bold line represents the mean rate of change in body mass.

found no support for the DPCH using data collected on temperate-breeding Kentish Plovers.

One of the primary assumptions of the DPCH is that early in the breeding season, food availability is sporadic and/or limited, resulting in the incubating adults being unable to meet their energetic requirements from exogenous sources, leaving them to rely on body stores (Erckmann 1983, Webb *et al.* 2002). Prey availability was not measured as part of this study; however, recent research has shown that prey availability on the northern breeding grounds of shorebirds is not limiting (Moltofte *et al.* 2007, Tulp & Schekkerman 2008). Furthermore, there may be three reasons why this assumption is not supported at my study site. First, if prey availability was very limited then males should not have been able to gain body mass

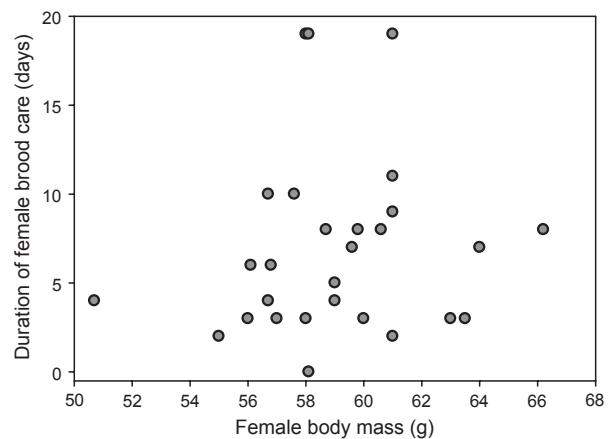


Figure 3. In Dunlins, there was no relationship between a female's body mass near the end of incubation and the number of days she provided brood care ($P > 0.05$).

during incubation, especially considering that breeding male Dunlins have substantially higher energetic costs than breeding females (> 25% higher daily energy expenditure; Tulp *et al.* 2009). There is also no reason why males should be more successful foragers than females, or that they are able to spend more time foraging. Secondly, Dunlins nesting in Alaska produce their eggs almost exclusively from exogenous resources accrued on the breeding grounds (Jamieson 2009), suggesting that there is sufficient food for producing eggs from exogenous means. Lastly, after nest loss, many females are able to lay replacement clutches quickly (mean = 9.3 days from nest failure to initiation of the replacement clutch, confidence limits = 8.4–10.2 days, $n = 17$; Jamieson 2011), which would presumably be difficult in an environment where prey are scarce.

The DPCH focuses heavily on female energetic costs while ignoring that of the males. This is likely to be one of the reasons why I failed to find any support for the first prediction that females will be in poorer condition than males in early incubation. Male Dunlins, like many sandpipers, have high energy costs prior to incubation. Males attract females and defend their territories using energetically expensive aerial displays (Ashkenazie & Safriel 1979) and the high costs of these displays could result in the males' poor condition at the beginning of incubation. A low body mass during the pre-incubation period may even be adaptive for males, as smaller males perform aerial displays more often and for longer periods than larger males

(Blomqvist *et al.* 1997). Additionally, due to their small size, males may have high thermoregulation costs upon arrival on the cold sub-Arctic breeding grounds (Lindström & Klaassen 2003). These large energetic expenditures prior to nesting may also help explain why males are gaining mass during incubation; they may be re-building energy stores spent earlier in the breeding season.

Males may also be gaining body mass not to recover from past body mass loss but to store energy for future use. In a study of five species of breeding shorebirds, Soloviev and Tomkovich (1997) found that adult body mass during brood rearing was lower than during incubation. During early brood rearing, much of an adult's daily schedule is devoted to parental activities such as brooding and vigilance (Ashkenazie & Safriel 1979). These activities can limit the amount of time an adult can dedicate towards self-maintenance. Such a time conflict is predictable, as is the fact that the female is likely to desert shortly after hatch; therefore it is plausible that selective forces have favoured male Dunlins that store endogenous reserves during incubation.

Body mass dynamics are not always related simply to endogenous reserve dynamics, and may be associated with phenotypic organ flexibility (Guglielmo & Williams 2003). Gonads are amongst the most flexible of the organs (up to 220-fold increase in size; Vézina & Salvante 2010). One may predict that body mass dynamics during the breeding season may be related to gonadal phenotypic flexibility. Mature gonads are costly to maintain (Vézina & Salvante 2010) and so it could be beneficial for them to regress shortly after mating. If gonadal regression strongly influenced body mass dynamics in Dunlins then mass should have declined during incubation in both sexes, albeit the decline would be more pronounced in females. However, the results show that neither sex lost weight during incubation.

Female Dunlins may maintain low body condition during incubation as a means of leverage during her negotiations with her partner over brood care investment. Barta *et al.* (2002) developed a state-dependent dynamic game model for parental care that considered how an individual may adjust parental care investment depending on its body condition, its mate's body condition, time in the season and probability of rebreeding within that season. Their model suggested that an individual's condition has a large effect on the amount of

brood care they provide and, more interestingly, that a female can 'force' her mate to care by strategically losing body mass. They concluded that a male mated to a female in poor condition will choose to care for the brood because the female is apt to desert so she can attempt to regain her condition and increase her probability of survival. The benefit to the male would be even greater in species with high mate fidelity, like the Dunlin (> 70%, C. van Leeuwen unpubl. data). If the female does not altogether desert her brood, the quality of her care may be poor because she would need to devote more time to self-maintenance and less time to brood care than a parent in good body condition. With this in mind, I suggest that a female Dunlin may maintain a low body condition as part of her strategy during negotiations with her mate over parental care. To test whether the female's body condition would truly affect her parental performance (i.e. whether low female body condition is a credible threat) it would be necessary to conduct a male removal experiment, thus forcing the females to care. The male must be removed close to hatching so the female has already put in her bid (i.e. lost weight) by the time the manipulation has occurred. One would predict that females who were in the best condition at the time of male 'desertion' would provide the highest quality of care and/or remain with the brood for the greatest amount of time.

Erckmann (1983) used similar logic when he proposed the DPCH to explain the evolution of male-biased care and polyandry in shorebirds. However, he suggested that, rather than strategic weight loss, females lost body mass because they were energetically stressed by egg production and poor feeding conditions. However, like Barta *et al.* (2002), he also proposed that after brood desertion a female may benefit by remating and laying a second clutch (i.e. double-brooding). Dunlins are capable of double-brooding (Soikkeli 1967). On the Yukon Kuskokwim Delta, 17% of individuals that hatched their first nest and deserted their offspring went on to double-brood and all double-brooders, except one, were females ($n = 6$; Jamieson 2011). Females that intend to double-brood may provide very little care to their original brood, while trying to maintain a relatively high body mass for a second breeding attempt (Griggio *et al.* 2005); such a strategy could obscure the relationship between brood care duration and female body mass. However, after I removed from the analysis

the three females that were known to double-brood, there was still no significant effect of female body mass on duration of maternal brood care.

In conclusion, it appears that the question of what influences the timing of brood desertion is far more complex than females simply caring until their physiological condition limits their ability to do so. This may be particularly true in species that double-brood. In such species, the duration of maternal brood care is most likely a balance of her survival, her mate's behaviour and physiological state, the needs of her first brood and the probability of finding a new mate and successfully rearing another brood.

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