# Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers

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Theoretical models predict that in species with obligate biparental care, individuals will partially compensate for decreased parental effort by their partners as a stable evolutionary strategy. Full compensation may occur when breeding success is an accelerating function of parental effort, especially in long-lived bird species. We experimentally examined the effect of time-depth recorders (TDRs) on body mass and parental behaviour of thick-billed murres, *Uria lomvia*, and evaluated the effect of TDRs as handicaps to test whether individuals compensate for decreased partner effort and whether compensation is sex biased. Compared with control birds, TDR-equipped birds had reduced body mass, offspring attendance, number of foraging trips and feeding rates, and males had increased foraging trip duration. In general, males lost mass at a higher rate and made longer foraging trips than females. Partners of TDR-equipped birds compensated for their mates' reduced parental effort by increasing offspring attendance and by increasing chick provisioning above average rates of control birds. Although partners of TDR-equipped birds fully compensated for their mates' reduced offspring attendance (i.e. chicks were never observed to be left unattended), total provisioning rates of pairs with a TDR-equipped bird ($\overline{X} \pm SE = 4.38 \pm 0.26$ meals/day) were significantly lower than those of control pairs ($5.74 \pm 0.31$ meals/day). However, fledgling success of control and TDR-equipped birds did not differ between reproductive seasons. TDR-equipped birds also had a significantly lower rate of return to breed than their non-TDR-equipped partners or control birds, and those that did return the following season were more likely to change mates (32%) compared with controls (0%). Taken together, our results underline the need to quantify the effects of monitoring equipment used to measure seabirds' activities, and indicate the ability of female and male thick-billed murres to compensate for reduced partner effort due to handicapping. Compensatory behaviour seems to be a necessary response of this single-brooded species to ensure current breeding success; however, it may affect the stability of pair bonds in some individuals.

According to life-history theory, animals will tend to minimize their effort during current reproduction to maximize survival and lifetime reproductive success (Williams 1966). In species with biparental care, both parents need to balance their allocation towards offspring care and self-maintenance in response to changing demands of energy and time during reproduction (Drent & Dann 1980; Ydenberg et al. 1994). Thus, conflicting interests in the level of contribution between partners are likely to occur. Game theory models predict that only partial compensation for a mate's reduced parental effort must occur to maintain a stable evolutionary strategy of biparental care (Houston & Davies 1985; McNamara et al. 1999). Thus, males and females should compete to provide a minimum parental effort within a reproductive season to maximize their individual fitness.

Empirical studies have tested these predictions using mate removal, testosterone implants and handicapping experiments in monogamous species. Mate removal studies have provided insights into the function of biparental care and monogamy across different taxa (birds: Bart & Tornes 1989; review of male-removal by Transue & Burger 1989; Møller 2000; beetles: Fetherston et al. 1994; Hunt & Simmons 2002; fish: Mrowka 1982; Lavery & Reebs 1994) and have shown that individuals' responses to the loss of their mates vary from abandonment to complete compensation of parental effort. Nevertheless, these

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experiments have failed to test dynamic models of bargaining of parental effort between males and females. Although experiments with testosterone implants (e.g. Saino & Møller 1995; Hunt et al. 1999; Alonso-Alvarez 2001) have been used to reduce paternal effort, female compensation is difficult to interpret because a female's behaviour can be affected by the endocrine manipulation of her partner (Alonso-Alvarez 2001). Handicapping experiments using birds have reduced parental effort of one member of the pair by attaching weights to tail feathers or clipping tail and flight feathers (Wright & Cuthill 1989, 1990; Whittingham et al. 1994; Markman et al. 1995; Sanz et al. 2000; Schwagmeyer et al. 2002), so the level of response of the other member can be measured. Some of these studies have found partial compensation for a partner's reduced effort (Wright & Cuthill 1989, 1990; Whittingham et al. 1994; Markman et al. 1995), supporting dynamic models, whereas others (Sanz et al. 2000) reported full compensation. A recent model of biparental care has proposed that full compensation may occur when breeding success is an accelerating function of parental effort; that is, in species with high predation levels, high breeding density or poor condition of one parent (K. M. Jones et al. 2002). Other studies have found a lack of compensation for reduced partner effort (Slagsvold & Lifjeld 1990; Saether et al. 1993; Schwagmeyer et al. 2002). Overall, these results suggest that further studies are required to better understand the dynamic of bargaining of effort levels between sexes.

Most handicapping experiments testing for compensatory behaviour have been performed in socially monogamous passerines and have used chick feeding as the only measure of parental care (but see Markman et al. 1995); only one has been reported for a seabird (Saether et al. 1993). Long-lived seabirds are thought to be less likely to increase their investment in current reproduction and risk affecting their future breeding (Curio 1988; Pugesek et al. 1990). On the other hand, seabirds' responses to reduced parental effort due to handicapping may be easier to interpret because confounding variables common in passerines, such as frequent extrapair copulations and multiple broods, are rare or absent.

Data loggers have been used extensively for the study of foraging behaviour of seabirds (e.g. penguins, review in Gales et al. 1990; Falk et al. 2000; Garthe et al. 2000; Mehlum et al. 2001; Shaffer et al. 2003), pinnipeds (e.g. Kooyman et al. 1976; Boness et al. 1994; Hooker et al. 2002), cetaceans (e.g. Ray et al. 1978; Frost et al. 1985; Croll et al. 2001) and turtles (e.g. Eckert et al. 1989; Minamikawa 2001). The attachment of external devices reduces swimming speed of both marine mammals and birds (Wilson et al. 1986) and increases hydrodynamic and aerodynamic drag during diving and flying (Obrecht et al. 1988; Bannash et al. 1994), which in turn increase energy expenditure and affect foraging performance (Wilson et al. 1986; Gessaman & Nagy 1988; Croll et al. 1992; Culik et al. 1994). Although few studies have tested the effect of such devices on parental performance using equipped and nonequipped animals, extended foraging trip durations have been reported in several species of penguins (Croll et al. 1991; Watanuki et al. 1992; Hull

1997; Ropert-Coudert et al. 2000; Taylor et al. 2001; but see Gales et al. 1990; Ballard et al. 2001) and in Antarctic fur seals, *Arctocephalus gazella* (Walker & Boveng 1995). In flying seabirds, alcids carrying radiotransmitters with external antennas (Wanless et al. 1988) or time-depth recorders, TDRs (Tremblay et al. 2003) make fewer nest visits, but no effects have been found in king cormorants, *Phalacrocorax albiventer* (Kato et al. 2000) or wandering albatrosses, *Diomedea exulans* (Shaffer et al. 2003). Thus, data loggers can be used as handicapping tools in species where they increase breeding effort.

Increase of workload due to instrumentation may be a special concern for large alcids, which have one of the highest wing loadings of any seabird species (Greenwalt 1962; Spear & Ainley 1997) as a trade-off of their excellent diving capacities. In fact, the intermediate chick development strategy shared by thick-billed murres, common murres, *Uria algae*, and razorbills, *Alca torda*, has been attributed to reduce high costs of chick provisioning at the breeding site (Gaston & Jones 1998).

Our study had two main objectives; one was to quantify the effect of external time-depth recorders on body condition and parental behaviour of female and male thick-billed murres rearing chicks. The second objective, which could only be fulfilled if the recorders handicapped the birds on which they were deployed, was to determine whether the partner of a TDR-equipped bird would compensate for a reduction in parental effort by a gear-encumbered mate and whether this behaviour was sex biased. We used brooding time and provisioning rates as estimates of parental care. In addition, posteffects on return rates, breeding success and mate fidelity were examined.

## METHODS

We studied a breeding colony of thick-billed murres nesting at island GC4, one of the six Gannet Islands on the low-Arctic coast of southern Labrador, Canada (53°56′N, 56°32′W). At the time of this study, the colony included about 150 pairs. A total of 62 pairs were followed during the brooding periods (June–August) for 2000, 2001, 2002 and 2003. Of these, we captured and affixed TDRs to 18 males and 22 females (one mate per pair) that were rearing chicks. We used two types of TDRs, MK7 (Wildlife Computers, Redmond, Washington, U.S.A.; 25 g, flat shape with pointed end) and LTD_100 (Lotek Marine Technology, St. John's, Newfoundland, Canada; 16 g, cylindrical shape with rounded end) that were similar in size (5–8 × 1–2 × 1–2 cm) and cross-sectional area (1.7–1.9 cm$^2$, 1.2–1.3% of the body area). Birds were captured using noose poles from the edge of the cliff above the colony. After capture, we measured each bird's mass to the nearest 10 g using a spring scale and marked all individuals with permanent (stainless steel) and temporary (colour) numbered bands. TDRs were attached to the back of feathers using three strips of black Tesa tape (Tesa Tape, Charlotte, North Carolina) cable ties and drops of cyano-acrylate glue (Hot stuff, San Luis Obispo, California, U.S.A.) under both ends of the device. We placed TDRs

on the backs of the birds to maintain the birds' centre of gravity (Kenward 1987) and balance the total mass during flying (Obrecht et al. 1988). We also arranged each bird's contour feathers so that part of the frontal and lateral edges of the device were covered to reduce drag during swimming (Bannash et al. 1994) and to allow normal preening of dorsal feathers. In addition, we used black, Tesa tape because it resembled the plumage colour of the birds and appears to reduce the frequency of pecking (Wilson et al. 1990). We recaptured birds after 1–4 days for TDR recovery, reweighed them and collected blood samples (0.5 ml) from the tarsus vein for sex determination by molecular DNA analysis (Fridolfsson & Ellegren 1999). Samples were stored in vials with 95% ethanol until analysis. During capture and recapture, both adults were present at the breeding site, so chicks were never left alone. We used this procedure to ensure chick safety and to reduce possible stress on adults. Handling time from capture to release was 5–8 min for both initial capture and recapture.

To quantify parental care of murres equipped with TDRs (16 males, 19 females) and their partners, we conducted behavioural observations before and after TDR deployment, and after TDR removal during 2000 and 2001. We simultaneously obtained the same information for a group of undisturbed birds without TDRs (control birds: 13 females, 13 males). Both groups of birds had chicks of similar ages, ranging from 1 to 15 days old. We conducted observations from a blind using binoculars and a zoom telescope between dawn and dusk (0400–2200 hours) during 3–15 days of the chick-rearing period. Breeding sites were scanned every 10 min and the presence/absence and identity of adults were recorded to calculate the time spent at the breeding site per day. The departure and arrival of adults and chick-provisioning events were recorded continuously to calculate feeding frequencies and foraging trip durations. To identify individuals before capture, we temporarily marked birds with picric acid (yellow) or fluorescent paint (green, pink and orange). We attached a small container (10 cc of marking liquid) to the tip of the noose pole so drops of the liquid could be delivered from above the birds without disturbing the colony. Birds were marked as if they were hit by falling guano, which is a normal occurrence in the colony, so disturbance caused by marking was minimal. The mark patterns, along with other life-history information were recorded on ID cards for quick reference. Nonequipped birds were captured twice (4–17-day interval) and manipulated during a similar time period as the TDR-equipped birds to determine rates of mass loss. These were marked with a field-readable, stainless-steel leg band and a colour band, and a blood sample was taken for sex determination (Fridolfsson & Ellegren 1999). The results of sexing were obtained after the season was finished (observers were blind to the sex of birds) and then matched with the ID cards to interpret behavioural data.

We monitored 30–43 pairs of nonequipped birds daily from hatching to fledging to quantify fledging success. The fledging success of TDR-equipped and control birds was measured during the current (all years) and following breeding season. A subsample of control, TDR-equipped

birds and their partners, individually marked with colour bands, were monitored during the following breeding season to measure subsequent return rates, and maintenance of pair bonds. We calculated return rate based on the birds that were present at the colony during incubation and brooding. We did not perform observations before the laying period.

## Data Analysis

To determine the effects of TDRs on body condition (mass loss) and parental behaviour (chick attendance, number and duration of foraging trips, feeding rates), we compared data between groups (control and TDR-equipped birds) and sexes. Measures of parental behaviour for individuals were averaged per day, and comparisons between groups were made using the same chick ages (up to 11 days). To quantify feeding compensation by partners, we first did a cross-sectional analysis of chick-provisioning rates between three groups (TDR-equipped birds, their partners and control birds), and also between sexes. Then, we did a longitudinal analysis of TDR-equipped birds and their partners to account for possible individual differences between groups. We made matched-pair comparisons of chick-provisioning rates of TDR-equipped birds, their partners and the pair (both parents) before and after the TDR was deployed. In addition, we made paired comparisons between the two previous stage categories (before versus after TDR deployed) and after TDR removal to determine possible differences in chick provisioning and compensatory behaviour. To calculate the average provisioning rates, we sampled each bird that was equipped with a TDR for the same number of days before and after TDR deployment and after TDR removal (range 1–4 days), for case of analysis. Finally, to compare the total chick provisioning between control pairs and pairs with TDR-equipped birds, we matched chick ages to the three deployment stages, before TDR deployed (up to 7 days), after TDR deployed (4–11 days) and after TDR removed (12–15 days).

For each individual, we calculated time spent at the breeding site per 24 h even though the observation period only covered the daylight hours (18 h). Previous studies have shown that thick-billed murres at the Gannet Islands do not make changes at night (I. L. Jones et al. 2002). In the present study, if a bird that was present at dusk was found the following morning with dirty plumage, suggesting that it did not leave the breeding site during the night, we added 6 h (dark time) to the observed time the bird spent at the breeding site during the day.

Analysis of foraging trips included trips with and without a fish delivered to a chick. It was not possible to distinguish between bathing trips and feeding trips because birds could return to the breeding site with a fish after absences of less than 10 min. The first foraging trip was usually performed by females, which normally spend the night at sea (I. L. Jones et al. 2002) and arrive at the breeding site in the early morning. Thus, to calculate the duration of the first foraging trip, we assumed that the birds started to forage right after sunrise (0330 hours). We

calculated chick provisioning as the number of meals per individual and per pair per day.

Statistical analysis was carried out using SPSS version 11.5. We used parametric tests (Student's $t$ test, ANOVA and paired $t$ test) to compare groups if the residuals met the assumptions for the general linear model (homogeneity and normality). We report 95% confidence intervals instead of estimates of statistical power to address the question of type II error (Hoenig & Heisey 2001). Multiple comparisons were undertaken using the post hoc Tukey HSD test. The chi-square test was used to compare two categorical proportions. Means are expressed $\pm$ SE of the mean. All comparisons were two-tailed, except where noted otherwise, and differences were considered significant when $P < 0.05$.

## RESULTS

### Interannual Fledging Success

The fledging success of thick-billed murres was high and did not differ between years (2000: 0.93 fledglings/breeding site, $N = 30$; 2001: 0.98 fledglings/breeding site, $N = 40$; 2002: 0.98 fledglings/breeding site, $N = 43$; ANOVA: $F_{1, 112} = 0.576$, $P = 0.564$). Based on these results, we pooled the data for the analysis of mass loss (2000–2002) and parental care (2000–2001).

### Effect of Time-depth Recorders on Body Mass and Parental Behaviour

#### Effect on body mass

The initial body mass of males (965 $\pm$ 10 g, $N = 32$) was higher than that of females (917 $\pm$ 9 g, $N = 37$; ANOVA: $F_{1, 67} = 13.01$, $P = 0.001$), but did not differ between control (948 $\pm$ 10 g, $N = 31$) and TDR-equipped birds (932 $\pm$ 10 g, $N = 38$; ANOVA: $F_{1, 67} = 1.347$, $P = 0.25$). The relative mass of the TDR to initial body mass was on average 2.7% and 2.4% for females and males, respectively. The rate of mass loss varied between control and TDR-equipped birds (ANOVA: $F_{1, 63} = 75.77$, $P < 0.0001$) and with sex ($F_{1, 63} = 4.93$, $P = 0.030$), and the interactive effect of the factors on mass loss was significant ($F_{1, 63} = 4.84$, $P = 0.031$). Further analysis of the main factors showed that mass loss rates were significantly higher on TDR-equipped males ($-27.01 \pm 3.02$ g/day, $N = 15$) and TDR-equipped females ($-18.15 \pm 2.54$ g/day, $N = 21$) than control males ($-3.98 \pm 0.64$ g/day, $N = 15$; ANOVA: $F_{1, 28} = 59.45$, $P < 0.0001$) and control females ($-3.94 \pm 0.95$ g/day, $N = 16$; ANOVA: $F_{1, 35} = 21.88$, $P < 0.0001$), respectively. TDR-equipped males lost mass at a higher rate than TDR-equipped females (ANOVA: $F_{1, 34} = 5.988$, $P = 0.020$), and within control birds, both sexes lost weight at a similar rate (males: $-3.98 \pm 0.64$ g/day, $N = 15$; females: $-3.94 \pm 0.95$ g/day, $N = 16$; ANOVA: $F_{1, 29} = 0.002$, $P = 0.97$).

Similar results were obtained when controlling for the initial mass of each bird. The mass loss ratio varied between groups (ANOVA: $F_{1, 63} = 73.01$, $P < 0.0001$) and sexes ($F_{1, 63} = 4.013$, $P = 0.049$). The interactive effect of

the factors on mass loss ratio was significant ($F_{1, 36} = 4.145$, $P = 0.046$). In both sexes, TDR-equipped birds had significantly higher mass loss ratios than control birds (ANOVA: females: $F_{1, 35} = 23.41$, $P < 0.0001$; males: $F_{1, 28} = 63.05$, $P < 0.0001$). Within groups, differences between sexes were only significant within TDR-equipped birds, with males losing proportionately more than females relative to their body mass (ANOVA: $F_{1, 34} = 5.018$, $P = 0.032$; Fig. 1).

Four of the TDR-equipped birds that were still brooding chicks (2 males, 2 females) were reweighed 7–14 days after the TDRs were removed. All birds, except for one female ($-3.5$ g/day), increased in mass (4.2 $\pm$ 0.4 g/day) after TDR removal.

#### Effect on foraging behaviour

Thick-billed murres performed 1–12 foraging trips per day, lasting between 10 and 720 min. Parents delivered one to six fish to their chicks per day. Males foraged mostly during the day (0600–1500 hours) and females before sunset (2200 hours) and after sunrise (0330 hours).

Individual provisioning rates of control pairs and pairs with a TDR-equipped member (with chicks up to 7 days old) were compared before TDRs were deployed to check for possible individual differences between groups. We found no significant interactive effect of the group and sex on chick provisioning (ANOVA: $F_{1, 114} = 0.083$, $P = 0.774$). Provisioning rates did not differ significantly between groups (control pairs: 2.46 $\pm$ 0.18 meals/individual/day, $N = 26$; pairs with a TDR-equipped bird: 2.21 $\pm$ 0.12 meals/individual/day, $N = 35$; ANOVA: $F_{1, 114} = 1.437$, $P = 0.233$) or sexes (females: 2.22 $\pm$ 0.14 meals/day, $N = 32$; males: 2.41 $\pm$ 0.15, $N = 26$; $F_{1, 114} = 0.755$, $P = 0.387$). The mean values of both groups (control and TDR-equipped birds) and sexes were within the 95% confidence limits (2.13–2.54 meals/day) of the grand mean.

To examine the effect of TDRs on chick-provisioning rates, chick attendance and number and duration of foraging trips, we compared the mean rates of control
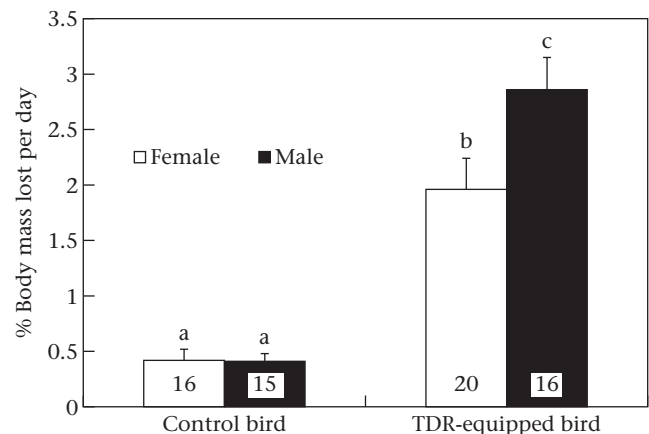


**Figure 1.** Mass loss (mass loss per body mass per day) of control and TDR-equipped thick-billed murres rearing chicks at the Gannet Islands, Labrador. Means $\pm$ SE. Different letters above bars denote statistical differences between groups (ANOVA: $P < 0.0001$).

(13 males, 13 females) and TRD-equipped birds (16 males, 19 females) using the same chick age categories (up to 11 days old). Provisioning rates of TDR-equipped birds were less than one-half of those of control birds (ANOVA: $F_{1, 57} = 70.33$, $P < 0.0001$). There was no difference in provisioning rates between sexes ($F_{1, 57} = 0.151$, $P = 0.699$) and no interaction between instrument status and sex ($F_{1, 57} = 0.295$, $P = 0.589$; Table 1). In control pairs, males and females did not differ significantly in their mean provisioning rates (ANOVA: $F_{1, 25} = 1.012$, $P = 0.324$; Table 1). Both male and female TDR-equipped birds performed fewer foraging trips per day than control birds (Table 1; ANOVA: TDR condition: $F_{1, 57} = 67.46$, $P < 0.0001$; sex: $F_{1, 57} = 0.187$, $P = 0.667$). No interactive effect of the factors on foraging trip was detected ($F_{1, 57} = 0.700$, $P = 0.406$).

Foraging trip duration varied between groups (ANOVA log-transformed data: $F_{1, 57} = 13.74$, $P < 0.0001$) and sexes ($F_{1, 57} = 36.91$, $P < 0.0001$, Table 1). There was not a significant interaction effect of group∗sex on trip duration (ANOVA: $F_{1, 57} = 3.263$, $P = 0.076$). Further analysis of the main factors was done due to the small $P$ value of the interaction term. Within sexes, TDR-equipped males performed longer foraging trips than control males (ANOVA: $F_{1, 27} = 15.498$, $P = 0.001$). However, the trip duration did not differ between TDR-equipped females and control females ($F_{1, 32} = 2.694$, $P = 0.111$). In both groups, males performed longer foraging trips than females (ANOVA: control: $F_{1, 24} = 14.90$, $P = 0.001$; TDR condition: $F_{1, 33} = 23.92$, $P = 0.0001$).

### Effect on brooding behaviour

Parents attended their breeding sites alternately during the chick-rearing period, which lasted 15–24 days. Most females brooded their chicks from early morning to late afternoon (overnight at sea) and most males brooded from late afternoon until the next morning (overnight at the breeding site). The duration of the chick-rearing period did not differ significantly between pairs with a TDR-equipped member ($20.69 \pm 0.43$ days) and control pairs ($21.15 \pm 0.54$ days; Student's $t$ test: $t_{37} = -0.643$, $P = 0.524$). The means of both groups were within the 95% confidence limits (20.17–21.54 days) of the grand mean.

Birds equipped with TDRs spent less time brooding their chicks than did control birds (ANOVA: $F_{1, 57} = 9.959$,

$P = 0.003$). Overall, males stayed with the chick proportionately more than did females for both groups (Table 1; ANOVA: $F_{1, 57} = 52.07$, $P < 0.0001$). There was no significant interaction between group and sex on brooding time ($F_{1, 57} = 1.375$, $P = 0.246$). Within sexes, TDR-equipped males spent significantly less time brooding than control males (ANOVA: $F_{1, 57} = 4.893$, $P = 0.036$). On average, TDR-equipped females stayed with the chick less time than control females, however, these differences were not significant ($F_{1, 57} = 3.491$, $P = 0.071$).

## Compensation of Reduction of Parental Effort

### Chick provisioning

We compared chick-provisioning rates between three groups (TDR-equipped birds, partners of TDR-equipped birds and control birds), controlling for possible sex differences, to determine whether partners would compensate for reduced parental effort by TDR-equipped birds. Provisioning rates differed significantly by group ($F_{2, 136} = 37.99$, $P < 0.0001$) but not by sex ($F_{1, 136} = 0.454$, $P = 0.502$; Fig. 2), and there was no interactive effect of the factors on the response variable ($F_{2, 136} = 1.149$, $P = 0.320$). Partners of TDR-equipped birds fed chicks at a significantly higher rate ($3.42 \pm 0.25$ meals/day) than did TDR-equipped birds ($0.87 \pm 0.12$ meals/day) or control birds ($2.60 \pm 0.15$ meals/day; Tukey HSD test: $P < 0.004$; Fig. 2). Comparisons of provisioning rates between the partners of TDR-equipped birds and control birds revealed that male partners of TDR-equipped birds had higher provisioning rates than control males (ANOVA: $F_{1, 52} = 10.70$, $P < 0.002$), but female partners of TDR-equipped birds did not differ from those of control females ($F_{1, 54} = 0.954$, $P = 0.333$; Fig. 2). However, the longitudinal analysis of pairs with a TDR-equipped bird (see below) showed that partners of both sexes increased their provisioning rates after TDR deployment.

To account for possible individual differences between pairs with a TDR-equipped member and control pairs, we used a longitudinal analysis to examine the effect of TDR deployment on chick provisioning. We made paired $t$ test comparisons before and after TDR deployment on 24 pairs of TDR-equipped birds and partners. The TDR-equipped

**Table 1.** Effect of externally attached time-depth recorders on parental behaviour of female and male thick-billed murres rearing chicks at the Gannet Islands, Labrador

| | Control birds | | | TDR-equipped birds | | |
|---|---|---|---|---|---|---|
| | Females | Males | Pooled | Females | Males | Pooled |
| Feeding/day | 2.7±0.27 | 2.5±0.24 | 2.6±0.18* | 0.9±0.13 | 0.9±0.22 | 0.9±0.12* |
| Foraging trips/day | 4.0±0.27 | 3.7±0.29 | 3.8±0.20* | 1.9±0.17 | 2.0±0.22 | 1.9±0.13* |
| Trip duration (h)† | 1.4±0.37 | 2.2±0.39* | 1.8±0.29* | 1.8±0.48 | 4.6±0.49* | 2.8±0.35* |
| Chick attendance (h) | 9.9±0.28 | 14.5±0.30* | 12.2±0.52* | 8.9±0.36 | 12.3±0.86* | 10.5±0.52* |

Means are given ± SE. Comparisons were done between groups (pooled data) and sexes (males and females) within each group. Significant differences between control ($N = 13$ females, 13 males) and TDR-equipped birds ($N = 19$ females, 16 males) and sexes are shown.
*Two-way ANOVAs: $P \leq 0.001$.
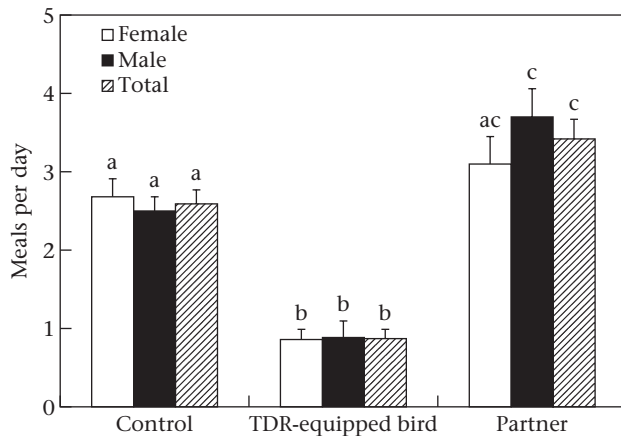†Data were log-transformed before the statistical analysis.

**Figure 2.** Overall effect of TDR deployment on chick provisioning in thick-billed murres at the Gannet Islands, Labrador. Data show feeding rates (mean $\pm$ SE) of TDR-equipped birds (19 females, 16 males), their partners and control birds (13 females, 13 males). Different letters above bars denote statistical differences between groups (two-way ANOVA: $P < 0.0001$).



**Figure 3.** Provisioning rates (mean $\pm$ SE) of TDR-equipped birds and their partners ($N = 20$ pairs) before and after TDR deployment, and after TDR was removed. Pair represents the total provisioning of TDR-equipped birds and their partners. Asterisks denote statistical differences between groups (paired $t$ tests: *$P \leq 0.003$; **$P < 0.0001$).

birds reduced their provisioning rates after TDRs were deployed ($t_{23} = 8.549$, $P < 0.0001$), whereas their unencumbered mates significantly increased their provisioning rates (before: $2.19 \pm 0.25$ meals/day; after: $3.55 \pm 0.31$ meals/day; $t_{23} = -4.084$, $P < 0.0001$; Fig. 3). For partners of TDR-equipped birds, both males (before: $2.51 \pm 0.43$ meals/day; after: $3.83 \pm 0.44$ meals/day; $t_{11} = -3.058$, $P = 0.011$) and females (before: $1.86 \pm 0.26$ meals/day; after: $3.26 \pm 0.43$ meals/day; $t_{11} = -2.661$, $P = 0.022$) significantly increased their feeding rates after TDR deployment.

We used a similar approach to determine whether chick-provisioning rates of TDR-equipped birds or their partners changed after the TDR was removed. The mean provisioning rates of previously TDR-equipped birds increased significantly ($t_{19} = -4.37$, $P = 0.001$; Fig. 3) to values similar to those before the TDR deployment ($t_{19} = 1.35$, $P = 0.194$). The partners of previously TDR-equipped maintained provisioning rates at the levels observed after TDR deployment ($t_{19} = 0.31$, $P = 0.79$), which were significantly higher than those before TDR deployment ($t_{19} = -3.75$, $P = 0.001$; Fig. 3). After TDR removal, the provisioning rates of the partners were significantly higher than those of the previously equipped birds (ANOVA: $F_{1, 39} = 14.36$, $P = 0.01$). There were no differences between males and females within each group (TDR-equipped birds: females $= 1.98 \pm 0.30$ meals/day; males $= 2.23 \pm 0.55$ meals/day; Student's $t$ test: $t_{18} = 1.02$, $P = 0.32$; partners: females $= 3.66 \pm 0.41$ meals/day; males $= 3.57 \pm 0.42$ meals/day; Student's $t$ test: $t_{18} = 0.78$, $P = 0.44$).

The pairwise comparisons for the total provisioning rates of pairs with a TDR-equipped bird revealed no significant differences before and after TDR deployment (paired $t$ test: $t_{19} = 0.986$, $P = 0.336$) and before TDR deployment and after TDR removal ($t_{19} = -2.044$, $P = 0.055$; Fig. 3). However, the provisioning of both parents was significantly lower after TDR deployment than after TDR removal ($t_{19} = -3.421$, $P = 0.003$; Fig. 3).
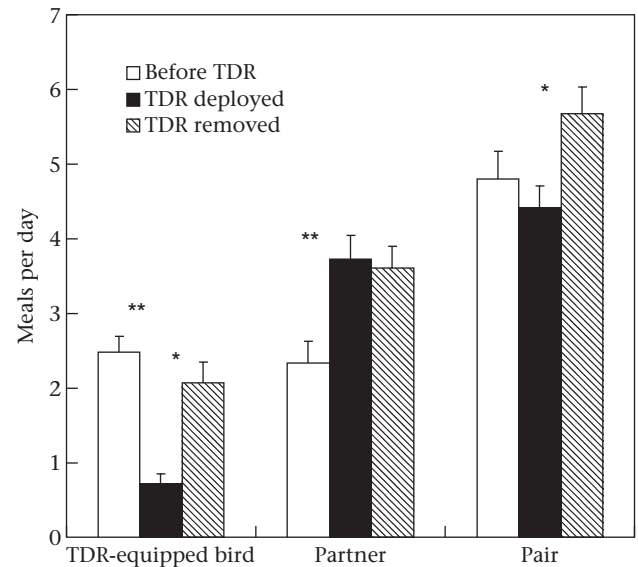
To compare the total chick provisioning of control pairs and pairs with a TDR-equipped bird before and after TDR deployment and after TDR removal, we matched chick age with TDR stage to control for age effects in both pair groups. Before TDR deployment, chicks were no more than 7 days old; during TDR deployment, chicks were between 4 and 11 days old; and after TDR removal, chicks were between 12 and 15 days old. The total chick provisioning per pair was not affected by whether a member of a pair was given a TDR (ANOVA: $F_{1, 133} = 3.758$, $P = 0.055$), but was significantly affected by TDR stage ($F_{2, 133} = 9.957$, $P = 0.0001$). There was no interactive effect of the factors on chick provisioning ($F_{2, 133} = 2.429$, $P = 0.092$; Fig. 4). A post hoc analysis revealed that pairs provided significantly less food before TDR deployment than after TDR deployment and TDR removal (Tukey HSD: $P < 0.05$). After TDRs were deployed, the pairs with a TDR-equipped bird provided significantly less food to their chicks than did control pairs (ANOVA: $F_{1, 62} = 10.988$, $P = 0.002$). However, there were no differences in the amount of food provided by the two types of pairs (control and TDR-equipped), when matched for chick age, before TDR deployment ($F_{1, 36} = 0.039$, $P = 0.845$) or after TDR removal ($F_{1, 35} = 0.520$, $P = 0.475$; Fig. 4).

*Offspring attendance*

The partners of TDR-equipped birds fully compensated for their mates' reduced offspring attendance (see above), such that chicks were never observed to be left unattended. To confirm these results, and also to account for possible individual differences between TDR-equipped birds, we used paired $t$ tests to compare offspring attendance of TDR-equipped birds and their mates before and after TDR deployment. The TDR-equipped birds reduced the time spent brooding their chicks after TDRs were
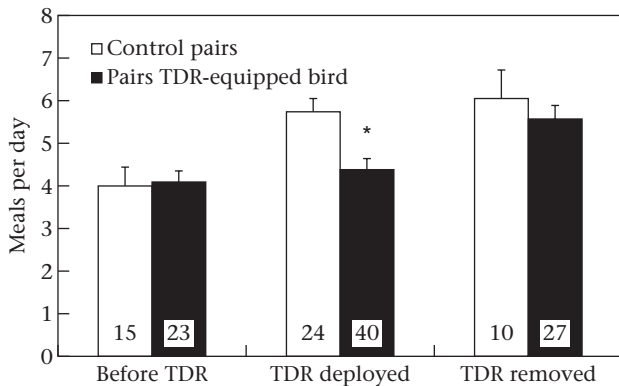
**Figure 4.** Total provisioning of control pairs and pairs with a TDR-equipped bird according to treatment stage (before TDR deployment, TDR deployed, and after TDR removal). Means are given ± SE. An asterisk denotes statistical difference between groups (ANOVA: $P = 0.002$).

deployed (before: $12.39 \pm 0.65$ h/day; after: $10.05 \pm 0.64$ h/day; paired $t$ test: $t_{23} = 3.462$, $P = 0.002$), whereas their unfettered mates increased their time significantly (before: $11.67 \pm 0.66$ h/day; after: $14.04 \pm 0.63$ h/day; $t_{23} = -3.666$, $P = 0.001$). Both sexes of the instrumented birds spent significantly less time at the breeding site after TDRs deployment (paired $t$ test: female: $t_{13} = 3.317$, $P = 0.037$; male: $t_9 = -2.676$, $P = 0.025$). For partners of TDR-equipped birds, females ($t_9 = -2.676$, $P = 0.025$) and males ($t_{13} = -2.332$, $P = 0.025$) significantly increased their time brooding the chicks after TDR deployment.

## Fledging Success

Of the 40 birds equipped with TDRs, three lost their chicks after deployment. One abandoned its breeding site 2 days after TDR deployment, another accidentally dislodged its chick during a fight with a neighbour and a third lost its chick for unknown reasons several days after the TDR was removed. Nevertheless, fledging success did not differ significantly between TDR-equipped birds (0.92 fledglings/year, $N = 39$) and control birds (0.92 fledglings/year, $N = 12$, Student's $t$ test: $t_{49} = 0.071$, $P = 0.994$). It was not possible to determine fledging success for one control and one TDR-equipped bird that were late breeders.

## Reproductive Costs

The rate of return to breed the following year was lower for TDR-equipped birds (83%, $N = 40$) than for control birds (96%, $N = 26$). The odds of return dropped significantly from 25:1 (TRD-equipped birds) to 4.74:1 (control) as expected (odds ratio = 0.181; chi-square test: $\chi_1^2 = 2.918$, one-tailed $P = 0.044$). Of the seven TDR birds that did not return to breed, three were females and four were males. In contrast, partners of TDR-equipped birds (88%, $N = 18$) returned to breed at a rate similar to that of control birds (chi-square test: $\chi_1^2 = 0.950$, $P = 0.329$).

Reproductive success did not differ significantly between control birds (0.89 fledglings, $N = 26$) and those equipped with TDRs the previous year (0.88 fledglings, $N = 33$; ANOVA: $F_{1, 58} = 0.014$, $P = 0.996$). Overall breeding success did not differ between TDR-equipped females (0.81 fledglings, $N = 21$) and males (0.89 fledglings, $N = 19$; Student's t test: $t_{38} = 0.740$, $P = 0.464$).

A subsample of control pairs ($N = 11$) and pairs with a TDR-equipped bird ($N = 19$) (both members individually banded) were followed the next year to determine mate fidelity. Of the pairs that had a TDR-equipped member the previous year, six changed mates the following year (2000: $N = 1$ of 5; 2001: $N = 4$ of 9; 2002: $N = 1$ of 5). All control pairs maintained their breeding sites and mates the following year (2000: $N = 4$; 2001: $N = 3$; 2002: $N = 4$). Overall, a significantly higher proportion of pairs with a TDR-equipped member (32%) bred with a different mate compared with control pairs (0%; chi-square test: $\chi_1^2 = 4.342$, $P = 0.037$). Only one of the 19 previously TDR-equipped birds bred the following year and that individual (a female) moved to a different breeding site. In contrast, most unencumbered partners (3 males, 2 females) bred with a different adult the following year and stayed at the same breeding site. Of these birds, two successfully fledged chicks, two lost their eggs/chicks and one bred very late in the season, so breeding success could not be determined.

The second year after TDR deployment, fewer birds that had been equipped with TDRs (68%, $N = 35$) were seen breeding at the colony compared with control birds (88%, $N = 26$; chi-square test: $\chi_1^2 = 3.34$, one-tailed $P = 0.034$). A similar proportion of males (3/14) and females (9/21) previously equipped with TDRs did not breed the following year. Of these 12 birds, six of their partners were individually banded and five of these were seen breeding with a different adult. Whether the birds equipped with TDRs were not seen because they changed their mates at the beginning of the season, omitted reproduction, or died was unknown.

## DISCUSSION

We were able to satisfy both initial objectives of this study on a long-lived seabird because we found clear negative effects of time-depth recorders on parental effort, thereby setting up the opportunity to examine compensatory parental behaviour experimentally using a handicapping approach.

## Effect of Time-depth Recorders on Parental Behaviour

Although our instruments were substantially less intrusive (3% of the body mass and 2% of cross-sectional body area) than the criteria (5%) used by most investigators for acceptable externally attached devices (Cochran 1980; Wilson et al. 1986) and were smaller and lighter than those used in previous murre diving studies (Croll et al. 1992; Falk et al. 2000), we found that instrumented thick-billed murres suffered a reduction in body mass,

offspring attendance, provisioning rates and frequency of foraging trips compared with nonequipped control birds, and that equipped males had longer foraging trip durations than equipped females or controls. Handling non-instrumented control birds similarly to the TDR-equipped birds eliminated the possibility that these effects were associated with stress due to manipulation.

Individual and interannual variation can also be excluded as factors that explain differences in foraging trip duration (Ballard et al. 2001) and provisioning rates of TDR-equipped birds. We found that foraging trips of equipped and control birds did not always end with chick feeding. In Cory's shearwaters, *Calonectris diomedea*, non-feeding visits are also a regular occurrence (Granadeiro et al. 1999). Thus, short or long foraging trips may in fact result in normal, reduced or no food delivery to chicks, so inferences about parental and foraging effort using only breeding site visits (e.g. I. L. Jones et al. 2002) and time spent at sea (e.g. Ballard et al. 2001) may lead to confusing conclusions. Additionally, the consistent findings with respect to provisioning rates using a longitudinal analysis before and after TDR deployment within a year and the cross-sectional analysis (control versus equipped birds) support the idea that a device effect was the main cause of reduced parental effort of TDR-equipped birds.

In short, we believe the most likely explanation for our results is the physical effect of the device on murre flight (Obrecht et al. 1988) and underwater swimming performance (Bannash et al. 1994). The associated increase in energy costs experienced by TDR-equipped birds during foraging (Gessaman & Nagy 1988) would have caused a reduction in body condition, and an increase in maintenance effort with a consequent reduction in parental care.

Previous efforts attempting to measure the effect of instrumentation on the behaviour of individual animals may have used inadequate measures (e.g. Cairns et al. 1987; Croll et al. 1992; Benvenuti et al. 1998; Falk et al. 2000; I. L. Jones et al. 2002). For example, we found that measures such as survival and success showed no difference between instrumented and noninstrumented birds, but parental behaviour was clearly affected. The tendency for partners to compensate seems to mask these effects on individual behaviour and total parental effort. Some studies that have tested the effect of TDRs in animal behaviour have found that individuals can compensate for the 'extra workload' without disrupting their parental performance (e.g. seals: Boyd et al. 1991; Harcourt et al. 1995; seabirds: Weimerskirch et al. 1995; Kato et al. 2000; Shaffer et al. 2003). Others have shown that breeding individuals that carry data loggers have extended foraging trips (penguins: Croll et al. 1991; Watanuki et al. 1992; Hull 1997; Ropert-Coudert et al. 2000; Taylor et al. 2001) and reduced chick provisioning (alcids: Wanless et al. 1988; this study). Recent efforts to reduce drag of instrumented birds during swimming and flying have used new attachment methods. Implanted data loggers seem to reduce the effect of externally attached devices in king penguin's, *Aptenodytes patagonicus*, foraging behaviour (Ropert-Coudert et al. 2000). However, these devices also affect the breeding success and survivorship of murres and

puffins, *Fratercula arctica* (Meyers et al. 1998; Hatch et al. 2000). Ventral attachment of TDRs seems to reduce physiological stress in common murres, but affects their frequency of nest site visits (Tremblay et al. 2003). The quantification of parental behaviour is a noninvasive method to infer gear effects on diving performance of free-ranging birds with external devices. Further research (i.e. using dummy TDRs) is required to determine the optimal size, mass and shape of instruments so that behaviour is not affected and reliable activity data can be collected.

## Compensatory Behaviour and Reproductive Costs

According to models of biparental care (Houston & Davies 1985; McNamara et al. 1999), only a partial compensation by individuals for a reduced parental effort of their partners is expected in a stable evolutionary strategy. Our results with respect to chick provisioning concur with these predictions and support other handicapping studies in birds (Wright & Cuthill 1989, 1990; Whittingham et al. 1994; Markman et al. 1995). We found that partners of encumbered murres increased their feeding rates above the average rates of control birds, so total amount of food delivered to chicks per day equalled that provided by both parents before TDR deployment. Even though this compensation was not enough in magnitude to equal the total provisioning rate of control pairs, it was sufficient for chicks to fledge at a rate similar to that of control birds.

In Antarctic petrels, handicapped birds also reduce chick-feeding frequency, however, nonmanipulated partners do not compensate for this reduction, and chick loss is higher than for control birds (Saether et al. 1993). Foraging costs may be significant for this species, which must travel long distances (400 km) during a prolonged chick-rearing period (45 days). We suggest that responses of seabird species to handicapping may be dependent on their life-history strategies and individual energy thresholds to different costs during reproduction (Jan-Ake 2002). In fact, handicapped thin-billed prions, *Pachyptila belcheri*, feed their chicks at a rate similar to that of control birds but incur a reduction in body mass as a result (Weimerskirch et al. 1995). Within seabirds, thick-billed murres have the shortest chick-rearing period at the breeding site (15–20 days) of any species except murrelets (*Synthliboramphus*; Gaston & Jones 1998) and can deliver only one fish at a time. Thus, birds must commute between foraging areas and the breeding site several times per day (Gaston & Jones 1998). The reduction in frequency of foraging trips and body mass of TDR-equipped birds suggests that chick provisioning is energetically costly. With only a single offspring at the breeding site, individuals face the prospect of zero reproductive success if they do not compensate for an indolent or disabled mate. A drastic reduction of chick provisioning may extend the chick-rearing period, or cause poor chick development and possibly increase the chances of mortality at departure (Gilchrist & Gaston 1997). We found that the

duration of the chick-rearing period by pairs with a TDR-equipped member did not differ from those of control pairs, which suggest maintenance of growth rates may be beneficial for both parents and offspring survival. Research on other auk species that provision chicks at the nest site until they are full-sized (e.g. puffins) would allow a better understanding of the mechanisms underlying compensatory behaviour.

After TDR removal, the previously equipped birds increased their feeding rates to values before TDR deployment. Their mates unexpectedly maintained their high provisioning rates, so the total amount equalled those of control pairs. After TDR removal, chicks were larger and received considerably more food than before TDR deployment compared with chicks in control nests. Thus, the magnitude of the recovery of TDR-equipped birds might not have fully met the feeding demands of larger chicks. A complete recovery of the instrumented birds and the consequent reduction of their mates' feeding rates seems to occur later on, but this prediction requires further study.

Contrary to partial compensation in chick provisioning, we found that partners of TDR-equipped birds fully compensated for a temporary daily reduction of offspring attendance by increasing their time at the breeding site. Chicks were never observed unattended. Because thick-billed murres breed in dense colonies where temporary abandonment is likely to yield chick mortality, full compensation is expected based on recent models of biparental care (K. M. Jones et al. 2002); that is, when breeding success is an accelerating function of parental effort (e.g. high nest site density and high predation levels). In yellow-legged gulls, *Larus cachinnans*, females mated to males with testosterone implants do not compensate for their mates' reduced incubation time (Alonso-Alvarez 2001). However, the fact that hatching success is not affected by a temporary abandonment of eggs suggests that compensatory behaviour is not crucial for chick survival.

Two surprising findings arise from our handicapping study. First, individuals were able to increase their parental effort above normal limits to cover their partner's deficiency when food availability was apparently normal. Second, the level of compensation to a reduced partner's effort (full or partial) was related to individual costs of males and females towards different aspects of parental care and the consequent likelihood of breeding failure.

Parental roles and levels of energy allocation are not necessarily equal between males and females in species with biparental care (e.g. Hamer & Furness 1993; Gray & Hamer 2001). Therefore, compensatory responses to reduced parental effort of impaired mates may also vary according to different parental roles between sexes (Sanz et al. 2000). Generally, parental behaviour of TDR-equipped male and female murres in this study was similarly affected by the strain imposed by the TDRs. Nevertheless, TDR-equipped males lost weight at a higher rate than TDR-equipped females. We also found overall that males, including control birds, spent more time at the breeding site and made longer foraging trips than females. These results suggest that foraging strategies may differ between the sexes in thick-billed murres as suggested by a previous study at Gannet Islands on this subject (I. L. Jones et al. 2002). However, chick provisioning did not differ between sexes in control pairs with chicks that were 4–11 days old. Males and females both responded similarly to the reduction in chick provisioning of their partners, and although females spent less time with the chicks, male and female partners of TDR-equipped birds fully compensated for the absence of their mates at the breeding site. Compensatory behaviour seems not to be related to parental roles, but to reproductive values and costs of increased parental effort for males and females.

Parents that provide biparental care have common and conflicting interests, and in theory, males and females are expected to compete to provide the minimum parental effort to ensure their individual fitness (Williams 1966). Our results are consistent with these predictions of dynamic game models of parental effort (Houston & Davies 1985; McNamara et al. 1999), but further suggest that in truly monogamous, long-lived species, compensatory responses of males and females to reduced partner effort is more flexible than expected, and is likely to be the result of their obligated biparental care and life-history strategies.

Several authors have suggested that long-term relationships in monogamous species can help to synchronize parental activities, reduce energy allocation in mating and therefore increase lifetime reproductive success (Cooke et al. 1981; Fowler 1995; see Black 1996, 2001). In this context, it would be advantageous for individuals of long-lived species to maintain the condition of their partners and ensure their survival, so compensation for reduced partner effort would be more likely to occur. Although we found that all thick-billed murres compensated for the reduction of parental effort of their handicapped partners, we also found that these birds tended to change mates between years, whereas control pairs showed total mate and site fidelity. Divorce in monogamous birds is more likely to occur if there is a reproductive failure or if one member of a pair shows poor quality as a parent (reviewed in Choudhury 1995; see Black 1996). This may explain our results in part because although breeding success of pairs with a handicapped bird was not affected, there was a clear reduction on parental performance by the TDR-equipped mate. Mates of less experienced or young birds are expected to change mates if their current mates show poor parental performance (thick-billed murres; Gaston & Hipfner 2000; other birds: Rowley 1983; Choudhury 1995). Thus, young birds (or others with recently established pair bonds) that are forced to compensate may subsequently divorce their 'poor-quality' mates to reduce costs in future breeding seasons. Several authors have suggested that divorce should be seen as a tactic by an individual to increase fitness (see review Choudhury 1995). However, for our study population, the lack of known-age birds and fitness information precludes us from making conclusions about these predictions. Another nonmutually exclusive explanation for the higher rates of divorce of pairs with a TDR-equipped member is the mortality of their mates. We found that previously TDR-equipped birds returned to breed less often than their

partners and control birds, which suggests that handicapping might have affected the survival of TDR-equipped birds. However, it is also possible that TDR-equipped birds returned to the colony at the beginning of the season but left when they failed to remate (before observations began).

In summary, individual thick-billed murres' body condition and behaviour were affected by carrying TDR data loggers. Both males and females were able to fully or partially compensate for a reduction of parental effort by their handicapped partners to ensure breeding success. Although compensatory behaviour appears to be a necessary response for breeding success in this single-brooded species, it might also affect the stability of pair bonds of some individuals.

## Acknowledgments

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