Resource allocation underlies parental decision-making during incubation in the Manx Shearwater

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ABSTRACT

For many bird species, trade-offs in resource allocation become stark during incubation, when caring demands put into direct conflict their investment in reproduction versus survival. We demonstrate the critical importance of resource allocation, here measured indirectly as body mass, for incubation behavior in the Manx Shearwater (*Puffinus puffinus*), a biparentally-caring seabird. Using daily measurements of body mass from breeding pairs in combination with field observations and remotely collected behavioral data, we examined how changes in mass related to nest attendance and foraging behavior. We furthermore tested whether this differed between the sexes and between pairs of different breeding experience. We found that while body mass predicted the probability that incubating birds would choose to temporarily desert the nest, incubation shift duration was ultimately set by return of the foraging bird. The trip durations of foraging birds in turn were primarily dictated by their body mass reserves on departure from the nest. However, foragers appeared to account for the condition of the incubating partner by returning from sea earlier when their partner was in poor condition. This key finding suggests that decisions relating to resource allocation may be made cooperatively within the breeding pair during incubation. Our results contribute to understanding the mechanisms by which individuals regulate both their own and their partner's incubation behavior, with implications for interacting with fine-scale resource availability.

Keywords: behavioral coordination, incubation, Manx Shearwater, parental care, parental investment, resource allocation, seabird

LAY SUMMARY

- During breeding, animals must strategically determine how much to invest in the competing demands of reproduction and survival, which has important consequences for behavior.
- When pairs expect to breed for multiple years, individuals may make decisions in cooperation with their partner to preserve energetic resources across the pair as a whole.
- Body mass reflects an individual's energetic reserves and therefore the resources available to allocate to reproduction and survival. Measuring body mass can therefore help researchers understand how and why animals make decisions relating to their behavior.
- We measured changes in body mass during incubation for the Manx Shearwater (*Puffinus puffinus*), a seabird species in which both parents care for the offspring. We were interested in how the maintenance of body mass relates to parental behavior, whether this differs between males and females, and whether parents behave cooperatively.
- We found that shearwaters determined their foraging trip durations during incubation based on a combination of their own body mass and that of the partner, providing evidence that parents factor their partner's condition into their decisions.

L'allocation des ressources sous-tend la prise de décision parentale pendant l'incubation chez *Puffinus puffinus*

RÉSUMÉ

Pour plusieurs espèces d'oiseaux, les compromis dans l'allocation des ressources deviennent difficiles pendant l'incubation, lorsque les demandes en soins mettent directement en conflit l'investissement dans la reproduction et la survie. Nous démontrons l'importance cruciale de l'allocation des ressources, mesurée ici indirectement par la masse corporelle, dans le comportement d'incubation de *Puffinus puffinus*, un oiseau marin dont les deux parents donnent

des soins. En utilisant des mesures quotidiennes de la masse corporelle des couples reproducteurs combinées à des observations sur le terrain et des données comportementales recueillies à distance, nous avons examiné comment les changements dans la masse sont liés à la présence au nid et au comportement de recherche de nourriture. De plus, nous avons vérifié si cela différait entre les sexes et entre les couples ayant des expériences de reproduction différentes. Nous avons constaté que si la masse corporelle prédisait la probabilité que les oiseaux incubateurs choisissent de déserter temporairement le nid, la durée de la période d'incubation était ultimement fixée par le retour de l'oiseau en quête de nourriture. La durée des sorties des oiseaux en quête alimentaire était quant à elle principalement dictée par leurs réserves corporelles au moment de leur départ du nid. Cependant, les individus en quête alimentaire semblaient tenir compte de la condition physique de leur partenaire d'incubation, en revenant de la mer plus tôt lorsque leur partenaire était en mauvaise condition. Ce résultat clé suggère que les décisions relatives à l'allocation des ressources peuvent être prises en coopération au sein du couple reproducteur pendant l'incubation. Nos résultats contribuent à la compréhension des mécanismes par lesquels les individus régulent à la fois leur propre comportement incubateur et celui de leur partenaire, avec des implications d'interaction par rapport à la disponibilité des ressources à une échelle fine.

Mots-clés: coordination comportementale, incubation, *Puffinus puffinus*, soins parentaux, investissement parental, allocation des ressources, oiseau marin

INTRODUCTION

To maximize lifetime reproductive output, parents should balance their resource allocation to current versus future breeding attempts (Trivers 1972) according to their placement on the life-history spectrum. While long-lived species, which exhibit a low reproductive rate, should invest conservatively in breeding in favor of survival, short-lived, high reproductive output species should invest in reproduction at the expense of future survival (Stearns 1992). When pairs expect to breed together for multiple years, exploiting the partner may come at a cost by reducing their ability to invest in future breeding attempts. In this situation, pairs may benefit from cooperating over their investment so that the costs of care are distributed more equally across the pair (Griffith 2019).

The allocation decisions an animal makes over its lifetime have significant consequences for its behavior, most notably during breeding (Boggs 1992). Furthermore, for biparentally-caring species, examining the relative contributions of each parent can give insight into whether and how allocation decisions are made cooperatively. Body mass is a good and measurable indicator of the available energetic reserves that individuals can allocate to survival or reproduction. Variation in mass impacts many aspects of reproduction. For example, body mass has been found to influence whether and when species choose to breed or provide care (e.g., asp viper [*Vipera aspis*], Naulleau and Bonnet 1996; Common Eider [*Somateria mollissima*], Jean-Gagnon et al. 2018, Bustnes et al. 2002), and can also influence the success of a breeding attempt (e.g., Black-browed Albatross [*Thalassarche melanophris*], Pinaud and Weimerskirch 2002; smooth snake [*Coronella austriaca*], Reading 2004). As such, measuring mass in different behavioral contexts might increase understanding about the strategic allocation of resources.

In birds, studying incubation behavior might provide insight into the optimization of life-history trade-offs, since incubation inevitably entails at least some degree of fasting for the caring parent. This ultimately leads to large fluctuations in body mass that must be managed to preserve reserves for the rest of breeding or future attempts. For species whose foraging grounds are far from the breeding site, such as seabirds, long bouts of fasting allow the other parent to spend substantial periods of time feeding at sea. Consequently, the regulation of body mass is especially important for these species. Procellariiform seabirds exhibit unusually long incubation shifts (Gaston 2004), which allow their partner to exploit distant, rich foraging sites. The regulation of body mass plays an important role in the scheduling and coordination of incubation shifts in many Procellariiform species (e.g., Southern Fulmar [*Fulmarus glacialoides*], Weimerskirch 1990; Blue Petrel [*Halobaena caerulea*], Chaurand and Weimerskirch 1994; Antarctic Petrel [*Thalassoica antarctica*], Tveraa et al. 1997; Storm Petrel [*Hydrobates pelagicus*], Bolton 1996; Gould's Petrel [*Pterodroma leucoptera*], Kim et al. 2018). Furthermore, many sexually-dimorphic seabirds exhibit sex-specific foraging and caring strategies that probably reflect differences in energetic constraints between males and females due to their differing size and, by extension, body mass (Clay et al. 2020, De Pascalis et al. 2020, González-Solís et al. 2000, Quillfeldt et al. 2004, Wakefield et al. 2009).

Seabird parents should manage incubation cooperatively (Jones et al. 2002). Failure to align shifts with the partner could excessively deplete body reserves if the incubating bird is forced to sit for long shifts, or could lead to breeding failure if it chooses to abandon the nest in search of food. Several burrow-nesting species are known to desert the nest temporarily before the partner has returned (henceforth "neglect"; Wheelwright and Boersma 1979), though it is unclear to what extent this reflects the condition of the incubating bird. The evidence that neglect is precipitated by reaching some lower mass threshold is equivocal, with some studies reporting clear evidence for such a set point (Herring Gull [*Larus argentatus*], Sibly and McCleery 1985; Blue Petrel, Chaurand and Weimerskirch 1994, Ancel et al. 1998)

and others finding none (Grey-faced Petrel [*Pterodroma macroptera gouldi*], Johnstone and Davis 2008; Cape Petrel [*Daption capense*], Weidinger 2008; Short-tailed Shearwater [*Puffinus tenuirostris*], Carey 2011; Gould's Petrel, Kim et al. 2018). Even short periods of neglect increase the risk of egg failure and predation (Boersma and Wheelwright 1979, Brooke 1990, Ronconi and Hipfner 2009), and although many seabird embryos are resistant to temporary chilling during incubation (Schreiber and Burger 2001), this will proportionally extend the incubation period (Ronconi and Hipfner 2009), increasing the parents' investment and potentially causing chicks to fledge at a suboptimal time (Perrins 1970, 2008). By sharing the costs of incubation with their partner, parents can minimize the risk that their partner decides to neglect.

The Manx Shearwater (*Puffinus puffinus*) is a Procellariform seabird that is an ideal candidate to investigate resource allocation during breeding in a long-lived species. Over the 51-day incubation period, Manx Shearwaters alternate incubation shifts of ~6 days (Harris 1966), during which time they lose ~15% of their body mass (Thompson 1987). The regulation of mass reserves is likely to be important in this species, both to ensure that parents are able to sustain the energetic chick provisioning period that follows hatching, and because birds that end breeding in poor condition are more likely to skip or fail the following year (Shoji et al. 2015a). While the patterns of incubation shifts have already been well described (Brooke 1990, Harris 1966, Thompson 1987), how this scheduling relates to fine-scale changes in body mass and the behavior of parents at sea has not been investigated. It is furthermore unclear whether male and female Manx Shearwaters differ systematically in their allocation decisions. Female Manx Shearwaters bear a greater initial cost of reproduction by producing the egg and are, on average, smaller than males (Brooke 1978). Perhaps as a consequence, they exhibit more tightly regulated food delivery to the chicks during the provisioning period than males (Hamer et al. 2006) and may take a smaller share in incubation (Brooke 1978, Harris 1966). However, the extent to which this influences sex-differences in incubation behavior is unknown. Finally, like many species (e.g., Kittiwake [*Rissa tridactyla*], Coulson 1966, Thomas 1983; Eurasian Oystercatcher [*Haematopus ostralegus*], van de Pol et al. 2006; Bearded Reeling [*Panurus biarmicus*], Griggio and Hoi 2011, Blue-footed Booby [*Sula nebouxii*], Sanchez-Macouzet et al. 2014), increased pair experience is associated with higher breeding success in the Manx Shearwater (Brooke 1978, Harris 1966). Whether this reflects better coordination of resource allocation between the partners, such that costs of incubation are more equally distributed, has not been investigated in this species.

Examining the decisions made by parents during incubation is important to the understanding of allocation and parental coordination, as this is a clearly energetically costly part of breeding in which the relative investments of each parent can be directly and easily measured. We investigated the relationship between body mass changes and incubation behavior for Manx Shearwaters over a 5-year observational study. We had 3 broad aims: (1) to examine how incubation is structured; (2) to explore how mass varies during incubation shifts and how this influences changes in neglect of the egg; and (3) to examine whether body mass predicts foraging trip duration and at-sea behavior.

As part of aim (1), we first explored whether colony-level behavior could explain patterns of incubation. In some seabird colonies, colony attendance is observed to be temporally aggregated across nests, which may reflect responses to endogenous rhythms and/or environmental conditions (e.g., Cruz et al. 2013, Huffeldt and Merkel 2016). We tested whether such aggregation occurred in Manx Shearwaters, and hence whether decisions are made at the level of the pair or reflect population-wide behavior. We then explored whether patterns in incubation—reflected in laying date, duration, number of shifts, and division of labor—varied with pair experience. We expected to observe higher breeding success or better coordination in experienced pairs.

For aim (2), we examined how mass declined during incubation shifts, whether this differed between the sexes, and whether this influenced shift duration and the decision to neglect. As one of the key indicators of the energetic reserves available to parents, we predicted that mass at the start of incubation would determine whether or not the incubating bird chose to neglect the egg. Furthermore, due to the smaller size and greater energetic investment of female Manx Shearwaters, we expected that they would invest proportionally less in incubation and would be more likely to neglect the egg.

Finally, as part of aim (3), we explored the role of body mass in determining foraging trip duration, how this related to mass gains on the trip, and what variables determine activity budgets for foraging shearwaters. Since incubation shifts typically end when the foraging bird returns to the nest, the duration of the incubation shift is usually determined by the decision of the foraging bird to return to the colony. We, therefore, expected the body mass of foraging shearwaters to play an important role in foraging behavior, and predicted that departure mass would determine the duration of the trip, the mass gains on these trips, and the amount of time dedicated to foraging.

METHODS

Study System

We collected data on the daily mass changes and behavior of 74 pairs of Manx Shearwaters breeding in a long-term study plot on Skomer Island, Wales (51°44′N, 5°17′W) during the incubation periods of 2015–2019 (Table 1). Egg

TABLE 1. Sample sizes used in each year for observations and GLS deployment. Numbers in parenthesis indicate individuals or nests that were not used in the previous year

Year		2015	2016	2017	2018	2019	Total (unique)
Nests		18 (18)	30 (28)	15 (9)	10 (6)	24 (13)	97 (74)
GLS	Individuals	19 (19)	9 (9)	0 (0)	6 (6)	26 (20)	60 (54)
	Nests	14 (14)	9 (9)	0 (0)	5 (3)	18 (14)	46 (40)

laying lasts from the end of April into early June. Incubation lasts for ~51 days (Michael Brooke 1990) and is split into shifts of 5–7 days, which are alternated between the parents, who exchange incubation duties during nocturnal colony visits. At the study plot, occupancy and breeding success of ~100 nests are monitored annually, which are accessed either through the natural nest entrance or via purpose-built inspection hatches. All individuals were identified with a permanent metal ring, provided by the British Trust for Ornithology. Table 1 gives sample sizes used in each year.

Sampling Methods

Individual identity, mass measurements, and pair experience. As part of the annual long-term monitoring, nests were checked daily for the presence of an egg during the laying period. When an egg was found, the sitting parent was identified using the metal ring, and its partner was identified when the pair later exchanged incubation duties. Females were sexed by cloacal inspection on the day the egg was found (Boersma and Davies 1987) and males by inference. From the point of laying to the day the egg hatched, all nests were checked at approximately 12:00 noon (to account for potential fluctuations in mass) to determine individual occupancy and to weigh the incubating bird using a 600-g Pesola spring balance, precise to 5 g. Where the egg was found unguarded, we continued to inspect the nest either until the egg was depredated or it was no longer possible for it to be viable (>10 days), at which point the nest was recorded as having failed. If either parent returned to the egg before this point, it was deemed to have been neglected. Occupancy, but not mass data, were collected in 2017. In total, 74 unique nests were used in the study (Table 1).

Pair experience was determined for each nest using historical breeding data. As the year in which the pair bond was initially formed was not known for many nests, experience was determined as either "new" or "experienced". Pairs were "new" when either individual had been observed nesting with a different partner in the previous year. Pairs that had bred together in the study year and at least one previous year were considered "experienced", and pairs that had only been observed once were designated "unknown".

Foraging behavior. To measure at-sea behavior, 54 individuals (Table 1) were fitted with light level geolocators (GLS; Migrate Technology Intigeo-C250 and Intigeo-C65)

with integral salt water immersion logging facility. GLS weighed 2.5 g, representing ~0.7% of body mass, and are not known to substantially impact foraging trip duration compared to untagged birds (Gillies et al. 2020). These were attached by two cable ties to a plastic ring on the tarsus to ensure immersion when on water (see Guilford et al. 2009 for details). GLS were deployed at the beginning of the breeding season and were retrieved either at the end of the same season or at the beginning of the following season.

The immersion logging function of geolocators was used to determine at-sea behavior. GLS tested for salt water immersion every 3 or 6 s, and recorded the number of samples immersed in each 5- or 10-min bin, respectively. These immersion data were used to classify behavior using previously verified threshold methods (Dean et al. 2013, Fayet et al. 2016) whereby we considered bins where <2% of recorded states were immersed as sustained flight, >98% as resting on the water, and intermediate values as foraging. The proportion of each 24-hr period (00:00–23:59) spent in each of the 3 behaviors was calculated.

Statistical Methods

Patterns in incubation. To determine intrinsic predictors of variation in lay date, we fitted a linear mixed model (LMM) to Julian lay date with the fixed effects of pair experience and year (model 1). We further examined the effects of pair experience, year, and breeding success on the duration of incubation in days (model 2) using a generalized linear mixed model (GLMM) with a Poisson error structure to account for the count-based response. Nests for which any of these parameters were unknown were excluded from the analysis, leaving 73 records across 58 nests.

To explore, in detail, variation in the patterns of incubation and how this is shared between the two parents, we examined how well sex and pair experience explained variation in the proportional contribution of the female to incubation (model 3), the number of shifts taken on by each parent (model 4), and the duration of the very first (model 5) and subsequent (model 6) incubation shifts. In model 6, we controlled for potential temporal changes in incubation behavior by including the fixed effect of "egg age", calculated as days since laying. Model 3 was fitted with a beta error structure to account for the proportional response variable; whereas models 4, 5, and 6 included count responses and so were fitted with a Poisson error structure. To control for the number of days parents had available to

them to take incubation shifts, model 4 included the additional fixed effect of incubation duration. We additionally attempted to replicate previous observational findings (Brooke 1978, Harris 1966) that males are more likely to take the first incubation shift, using a two-tailed binomial test that compared the observed proportion of first shifts taken by the female to a null expectation of 0.5. For these analyses, we removed nests where data on the first incubation shift had not been recorded, leaving 62 records for 52 nests.

We determined to what extent the duration of incubation shifts might be constrained by the duration of the shift preceding it by calculating the correlation coefficient between consecutive incubation shift durations using the package *rmcorr* (Bakdash and Marusich 2017). We computed a repeated measures correlation between the duration of an incubation shift and the duration of the previous shift for each burrow in a given year.

To examine whether colony-level aggregation in nest attendance might occur in Manx Shearwaters, we compared the distribution of changeover events (points at which the two parents exchange nesting duties) across the entirety of incubation to a null distribution of changeovers. If shearwaters return to the colony in an aggregated way, we would expect to observe that nights with intermediate numbers of changeovers are less frequent than expected by chance, since this implies that most nights either have many changeovers or very few, and hence there is some colony-level synchronicity in visitation. This is the equivalent of examining whether nights with very high or very low numbers of changeovers are more frequent than we expect by chance. To this end, for each year we measured the proportion of nights on which there were 0 changeovers, and compared this to the expected number of nights with 0 changeovers if nests were behaving randomly. We randomly sampled incubation shifts lengths with the replacement for the same number of birds, beginning incubation at the same time and in the same year. This allowed us to account for the differing number of nests actively incubating across the dates included in the study (owing to variation in phenology) and to account for the aggregation that may be driven by similar lay dates and subsequent incubation shifts. If a larger number of nights with very few changeovers exists in the real data than the randomly drawn data, this suggests that shearwaters are aggregating their visits to the colony temporally, while fewer low numbers would suggest that shearwaters have roughly equal colony attendance across nights and thus are unlikely to be responding to similar cues. To assess whether putative aggregation in the real data was significant, we measured whether the real proportion of nights with 0 changeovers fell outside the 95% quantile range of 10,000 randomly shuffled colony incubation periods, separately for each year. A two-tailed P-value was hence

calculated as the proportion of randomly shuffled incubation periods in which the observed value fell within the 95% quantile range.

Mass changes during incubation. We explored how mass varied over both single shifts of incubation and the incubation period in its entirety. We investigated what factors influenced the mass at which parents began their incubation shifts (model 7), and the rate of mass decay during these shifts (model 8). Where gaps were present in the daily mass data for individuals, they were linearly interpolated based on the current trajectory of mass loss for the incubating bird. We excluded individuals for which we had been unable to collect mass data, leaving 103 individuals across 52 nests. To test our prediction that a parent's mass at the start of the incubation shift would predict neglect behavior, we modeled the relationship between starting mass and the decision to neglect (model 9) using a binomial GLMM. For those shifts that ended in neglect ($N = 43$ across 21 individuals), we additionally explored whether the duration of time parents incubated for before they abandoned the nest was predicted by their mass (model 10) using a Poisson GLMM. Finally, we used a binomial GLMM to determine whether the number of days of neglect predicted the likelihood of egg hatching, using all nests for which we had neglect and breeding success data ($N = 73$ records for 58 nests; model 11).

Foraging behavior. To determine whether there was any evidence for cooperative behavior in decision-making during incubation in Manx Shearwaters, we investigated whether the two-way interaction of mass of the incoming bird and mass of the outgoing bird, as well as sex, predicted foraging trip duration using a generalized additive model (GAM) to account for a potential non-linear relationship (model 12). This analysis included 65 nests for which we had mass data for both parents. We further examined how well starting mass, sex, foraging trip duration, and time spent foraging predicted foraging gains as a percentage of body mass (model 13). All 54 GLS-carrying individuals were used in this analysis. The aim was to disentangle the factors that the pair might respond to to coordinate incubation stints, so as to reduce both egg neglect and the risk of excessive mass loss, which might have a long-term impact on their condition or survival.

To determine how mass loss during incubation shift might subsequently affect at-sea behavior, we modeled the proportion of time spent in each behavior state as a function of starting mass and trip duration, using separate beta GLMMs (model 14/15/16) for each behavior. It might be expected that differences in the proportion of time dedicated to specific behaviors could arise due to differences in relative commuting time: shorter duration trips, for example, may exhibit more flight behavior as a greater proportion of the trip was spent traveling to the foraging locale (Dean et al. 2013). To account for this possibility,

TABLE 2. Model structures for analysis. Model numbers are referenced in the text

Type	Model	Response	Fixed	Random
			Parameters	
Patterns in incubation				
LMM	1	Julian lay date	Exp + year	Nest
Poisson GLMM	2	Total incubation duration	Exp + outcome + year	Nest
Beta GLMM	3	Proportional share of incubation	Exp + sex + year	Nest
Poisson GLMM	4	N shifts	Exp + sex + year + inc dur	Nest
Poisson GLMM	5	Shift duration – shift 1 (days)	Exp + sex + year	Nest: ID
Poisson GLMM	6	Shift duration – all others (days)	Exp + sex + year + egg age	Nest: ID
Mass changes during incubation				
LMM	7	Start mass (g)	Exp + sex + year + egg age	ID
LMM	8	Daily mass decline (% body mass)	Exp + sex + year + egg age + shift day	ID
Binomial GLMM	9	Probability shifts ends in neglect	Exp + sex + year + egg age + start mass + shift dur	ID
Poisson GLMM	10	Shift duration following neglect	Exp + sex + year + egg age + start mass	ID
Binomial GLMM	11	Probability of hatching	Exp + year + days neglect	Nest
Foraging behavior				
Poisson GAMM	12	Foraging trip duration (days)	s (Start mass * partner mass) + sex + year	ID
LMM	13	Percentage daily mass gain	Start mass + sex + trip dur + prop forage + year	ID
Beta GLMM	14/15/16	Proportion of trip spent foraging/resting/flying	Start mass + sex + trip dur + prop commute + year	ID

Abbreviations: exp = pair experience, experienced or new; nest = nest identity; outcome = of incubation, hatched or failed; sex = male or female; inc dur = total duration of the incubation period, days; ID = individual identity; shift day = day of the incubation shift; start mass = mass of incubating bird at beginning of incubation shift, g; shift dur = duration of the incubation shift; partner mass = partner mass at start of corresponding incubation shift, g; trip dur = foraging trip duration, days; prop forage = proportion of each day spent foraging; prop commute = proportion of trip spent commuting.

we included a dummy variable of "proportion commuting time", assuming that the first and last days of the trip would be mostly comprised of commuting.

Statistical analyses were carried out in R version 3.5.1 (R Core Team 2021). The R package *lme4* (Bates et al. 2015) was used to construct LMMs and GLMMs, and beta GLMMs were constructed using the *glmmTMB* package (Magnusson et al. 2020). We assessed model fit through visual inspection of residual plots. *P*-values were obtained by comparing models to null models without the effect of interest using a likelihood ratio test. For categorical variables, least squares means for each level of the factor were calculated using the R package *emmeans* (Lenth et al. 2018). To account for repeated measures and any systematic variation that might be attributed to year, all models were fitted with individual and/or burrow ID, nested within year as appropriate, as a random (intercept only) effect. All model structures can be found in Table 2. Data are presented as means and 95% confidence intervals (95% CIs) unless otherwise specified.

RESULTS

Patterns in Incubation
For brevity, all statistical values for this section can be found in Table 3.

The average date of laying was 15th May, but year had a significant effect on this date, probably driven by 2018 when eggs were laid on average 4 days later than normal (19th May; Supplementary Material Table 1 and Supplementary Material Figure 1). New pairs laid their eggs slightly later than experienced pairs but this was not significant (mean date new: 16th May, experienced: 13th May).

Mean incubation duration for nests that hatched eggs was 50.9 (95% CI: 48.4, 53.6) days. There was no difference in duration for experienced vs new pairs, nor was there any variation associated with year.

Males took a greater proportional share of the incubation period than females (male: 0.53, 95% CI: 0.51, 0.55; female: 0.47, 95% CI: 0.45, 0.49); this did not vary with pair experience or age. Despite the greater overall contribution of males, males and females did not differ in the number of incubation shifts they took on (male: 4.20 [95% CI: 3.55, 4.85] shifts, female: 4.06 [95% CI: 3.55, 4.785] shifts). There was no difference in shift number between experienced and new pairs (experienced: 3.94 [95% CI: 3.41, 4.47] shifts, new: 4.32 [95% CI: 3.49, 5.15] shifts) and no effect of year.

Females took the first incubation shift in 39.74% of breeding attempts, versus 60.25% for males, but these proportions were not found to be statistically significant (two-sided binomial test: *P* = 0.09). However, when the first shift of incubation was taken by the female, this was

TABLE 3. Statistical values for likelihood ratio tests comparing models outlined in Table 2 to null models without the effect of interest. Exp = pair experience. Significant effects in bold; sizes reported in Results: Patterns in incubation

	Response	Exp (df = 1)	Sex (df = 1)	Year (df = 4)	Egg age (df = 1)
1	Lay date	**$\chi^2 = 3.48$, $P = 0.06$**		**$\chi^2 = 16.27$, $P = 0.003$**	
2	Incubation duration	$\chi^2 = 0.81$, $P = 0.37$		$\chi^2 = 0.55$, $P = 0.97$	
3	Proportion share	$\chi^2 = 0.00$, $P = 1$	**$\chi^2 = 18.25$, $P < 0.0001$**	$\chi^2 = 0.00$, $P = 1$	
4	N shifts	$\chi^2 = 0.74$, $P = 0.39$	$\chi^2 = 0.15$, $P = 0.70$	$\chi^2 = 7.37$, $P = 0.12$	
5	Shift duration (1)	$\chi^2 = 0.23$, $P = 0.63$	**$\chi^2 = 8.52$, $P = 0.004$**	**$\chi^2 = 14.40$, $P = 0.006$**	
6	Shift duration (all – 1)	$\chi^2 = 0.30$, $P = 0.58$	$\chi^2 = 2.52$, $P = 0.11$	$\chi^2 = 7.58$, $P = 0.11$	$\chi^2 = 0.08$, $P = 0.78$

TABLE 4. Statistical values for likelihood ratio tests comparing models outlined in Table 3 to null models without the effect of interest. Exp = pair experience. Significant effects in bold; sizes reported in Results: Mass changes during incubation

	Response	Exp (df = 1)	Sex (df = 1)	Year (df = 1)	Egg age (df = 1)	Day of shift (df = 1)	Start mass (df = 1)	Shift duration (df = 1)	Days of neglect (df = 1)
7	Start mass	**$\chi^2 = 4.53$, $P = 0.03$**	**$\chi^2 = 29.13$, $P < 0.0001$**	**$\chi^2 = 16.11$, $P = 0.001$**	**$\chi^2 = 8.16$, $P = 0.004$**				
8	Mass loss/day	$\chi^2 = 1.41$, $P = 0.23$	$\chi^2 = 0.41$, $P = 0.07$	$\chi^2 = 4.35$, $P = 0.24$	$\chi^2 = 3.17$, $P = 0.08$	$\chi^2 = 2.83$, $P = 0.09$			
9	P (neglect)	$\chi^2 = 2.14$, $P = 0.14$	$\chi^2 = 2.89$, $P = 0.09$	$\chi^2 = 3.00$, $P = 0.40$	$\chi^2 = 0.18$, $P = 0.67$		**$\chi^2 = 7.81$, $P = 0.005$**	$\chi^2 = 1.70$, $P = 0.19$	
10	Time to neglect		$\chi^2 = 1.48$, $P = 0.22$		$\chi^2 = 0.30$, $P = 0.59$		**$\chi^2 = 10.05$, $P = 0.002$**		
11	P (hatch)	$\chi^2 = 0.61$, $P = 0.44$		$\chi^2 = 3.57$, $P = 0.47$					**$\chi^2 = 22.02$, $P < 0.0001$**

significantly shorter (male: 4.06 [95% CI: 3.27, 5.05] days; female: 2.63 [95% CI: 1.96, 3.53] days), though notably, in all subsequent shifts, males and females were not found to differ in duration (male: 5.44 [95% CI: 4.93, 5.99] days; female: 5.10 [95% CI: 4.61, 5.63] days). Incubation shift duration additionally did not change over the course of incubation, nor was there an effect of pair experience (first shift: experienced: 3.40 [95% CI: 2.74, 4.23] days; new: 3.14 [95% CI: 2.30, 4.30] days; all shifts: experienced: 5.38 [95% CI: 4.92, 5.89] days; new: 5.15 [95% CI: 4.47, 5.94] days). Year had a significant effect on the duration of the first incubation shift, possibly due to the very short first incubation shifts observed in 2019, at 2.38 [95% CI: 1.81, 3.12] days (Supplementary Material Table 1).

There was a significant correlation between the duration of an incubation shift and the duration of the previous shift by the partner (Pearson's correlation coefficient = 0.26 [95% CI: 0.12–0.40]; $P = 0.0004$). The temporal aggregation of changeover events across study nests during incubation was not greater than random, suggesting there was no synchrony in nest visitation across the colony ($P = 0.71$, n iterations = 10,000 per year).

Mass Changes During Incubation
For brevity, all statistical values for this section can be found in Table 4.

Males began their incubation shifts at a higher mass than females (male: 459 [95% CI: 452, 465] g, female: 435 [95% CI: 429, 442] g), reflecting the sexual size dimorphism of this species (Brooke 1990). Individuals from experienced pairs began their incubation shifts at a higher mass than those in new pairs (experienced: 452 [95% CI: 447, 457] g; new: 442 [95% CI: 434, 450] g). The mass at which parents began their incubation shifts increased slightly over the duration of the incubation period, and equally for both males and females. Starting masses increased by 0.21 [95% CI: 0.07, 0.35] g for each day since the egg was laid (Supplementary Material Figure 2), such that the overall mean difference in starting mass between the last and first shifts was 8.81 g. Year had a significant effect on starting masses, possibly as masses in 2016 were particularly high (Supplementary Material Table 1).

Incubating birds lost 2.31 ± 0.17% of their body mass each day, equating to a decline of 10.03 ± 7.42 g daily. This daily mass decay did not differ between males and females (male: 2.71% per day [95% CI: 2.60, 2.82], female: 2.75 % per day [95% CI: 2.64, 2.86]), and was consistent over both the scale of a single incubation shift and the incubation period in its entirety. There was no effect of experience or year on the body mass declines experienced by parents.

Over the 5-year study period, 8.26% of incubation shifts ($N = 80$) ended in neglect. The probability that an incubation
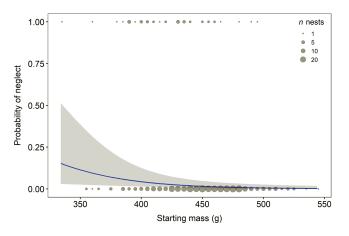
FIGURE 1. Incidence of neglect as a function of starting mass (g). Grey shaded area indicates 95% confidence intervals of model-estimated regression line (blue). Grey points indicate real shifts that ended in neglect (1) or did not (0) according to starting mass; point size indicates number of nests represented by datapoint according to legend inset.

shift ended in neglect was significantly predicted by the mass at which the incubating parent began incubation (Figure 1). The estimated coefficient for this parameter was 0.98 [95% CI: 0.96, 0.99] for each gram increase in starting mass; this is a log odds ratio owing to the logit link in the GLMM and in real terms equates to an approximate reduction in the probability of neglect of 7.10% for a 50-g increase in mass. The duration of the incubation shift, sex, and egg age had no effect on the probability of neglect. However, new pairs were more likely to neglect than experienced pairs (experienced probability: 0.03 [95% CI: 0.01, 0.06], new: 0.05 [95% CI: 0.02, 0.14]). For those shifts that ended in neglect ($N = 43$), the mass at which a parent had begun its shift predicted how long it sustained incubation before neglecting the egg, with heavier birds remaining at the nest longer before departing for sea (Figure 2). The number of days parents remained at the nest before neglecting increased by 1.15 [95% CI: 1.07, 1.22] % for each gram increase in starting mass; this corresponds to an increase in shift duration of 1.29 days for an increase in mass from 350 g to 400 g. Males and females remained at the nest for similar lengths of time before neglecting the egg (Figure 2).

Each day of neglect decreased the odds of hatching; the estimated log odds ratio coefficient for this parameter was 0.45 [95% CI: 0.23, 0.85]. The effect of neglect on hatching success showed diminishing returns over time: while 2 days of neglect reduced the probability of hatching to 18.43% compared to 71.88% for no neglect, the difference in hatching probability between 15 and 13 days of neglect was <0.0001% (Figure 3). Pair experience and year had no effect on the probability of hatching.

Foraging Behavior
Foraging trip duration was predicted by the smoothed two-way interaction between mass at the beginning of
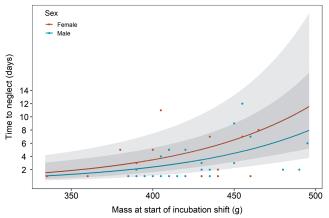

FIGURE 2. Number of days until neglect occurred as a function of mass at the start of the incubation shift (g) for females (orange) and males (blue). Grey shaded areas indicate 95% confidence intervals of model-estimated regression for females (orange line) and males (blue line) separately. Confidence intervals plotted with 50% opacity; darker areas indicate overlap.
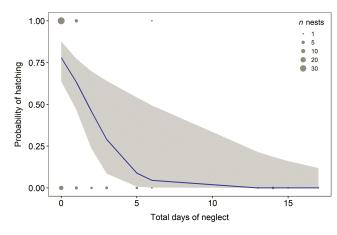

FIGURE 3. Probability of hatching as a function of days of neglect. Grey shaded area indicates 95% confidence intervals of model-estimated regression (blue line). Grey points indicate actual nests where the breeding attempt was successful (1) or not (0) according to the number of days the parents neglected the egg for; point size indicates number of nests represented by datapoint according to legend inset.

the incubation shift and partner's mass (EDF = 3.16, $\chi^2 = 28.00$, $P < 0.0001$). The longest foraging trip durations were observed for light birds whose partners were in good condition; foraging trip duration decreased with both increasing start mass and decreasing partner mass (Figure 4). There was no effect of year ($\chi^2 = 1.78$, $P = 0.75$) or sex on trip duration (male: 6.28 [95% CI: 5.83, 6.69] days, female: 6.20 [95% CI: 5.74, 6.69] days; $\chi^2 = -0.35$, $P = 0.54$).

Over their entire foraging trips, shearwaters gained a mean 12.63 ± 9.24 % of their body mass, corresponding to approximately 50.00 ± 33.89 g (mean ± standard deviation). Birds that began their foraging trips at a higher mass
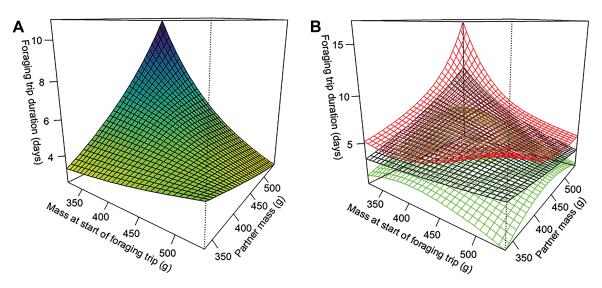
FIGURE 4. (**A**) Perspective plot of predicted foraging trip duration (days) as a function of the smoothed two-way interaction of mass at the start of the foraging trip (g) and the mass of the partner (g). (**B**) Confidence intervals of the predictions, where red = +2 standard errors from prediction surface, green = −2 standard errors from prediction surface, and black = prediction surface.

had lower percentage foraging gains on their trips: birds gained less mass per gram increase in their starting mass (see Table 5 for test statistics and parameter estimates). Males were found to gain a greater percentage of mass on their trips. Total mass gained foraging was not related to foraging trip duration or the amount of time the bird spent foraging.

During their foraging trips, birds spent 42.25 ± 10.87% of their time foraging, 39.90 ± 14.43% of their time resting, and 17.86 ± 13.02% of their time in flight. The mass at which a bird began foraging significantly predicted the time it spent foraging and resting: heavier birds spent less time foraging, and more time resting (Table 6, Figure 5), such that a bird weighing 400 g would reduce foraging time by 6.00% and increase resting time by 7.05% compared to a bird weighing 350 g. We did not find evidence for a relationship between mass and flight behavior.

DISCUSSION

While incubation is a clear opportunity for parents to employ a cooperative turn-taking approach to providing care, it is not well understood what underlies the decision of foraging parents to return to the nest, or for incubating parents to temporarily or permanently desert the nest. Here we demonstrate the critical importance of changes in parental body mass and reserves for incubation behavior in the Manx Shearwater. While incubating birds appeared to respond principally to the return of their partner from sea, we found that foraging trip duration was mostly driven by the requirement of the foraging bird to recoup its lost body mass, with those birds that departed the nest at a lower mass spending a proportionally longer time at sea. Similar results have been reported for Storm Petrels (Bolton 1996), Little Penguins (*Eudyptula minor*; Kato et al. 2008), and Short-tailed Shearwaters (Carey 2011), and probably reflect the importance of regulating energy reserves for these long-lived species. However, although the principal determinant of foraging trip duration was the mass of the outgoing bird, we also found that departing birds whose partners were in good condition took correspondingly longer trips, matching previous findings in this species (Gillies et al. 2021), and suggesting that shearwaters take a more cooperative approach to incubation behavior.

The mass losses sustained by incubating shearwaters had clear implications for their subsequent foraging behavior, with birds that ended their shift at a lighter mass spending more time at sea and exhibiting greater foraging gains, suggesting individuals try to maintain their mass at a particular baseline. During their trips, heavier birds spent less time foraging and more time resting, mirroring previous findings for shearwaters whose breeding investment was experimentally reduced, and which were therefore probably in better condition (Fayet et al. 2016). This effort could reflect each individual's optimal balance between mass gains and limits to energetic expenditure. If birds have less mass to gain, it may be beneficial to invest less in the highly energetic activity of foraging, and instead spend more time resting. Decisions when to rest and when to forage may be employed strategically, so that as the bird approaches good condition it pays only to explore better foraging opportunities, and to pass up less profitable ones by resting. Shortening the duration of the trip itself may not be an optimal way to conserve energy, both because shearwaters are constrained to return to the colony at

TABLE 5. Test statistics and parameter estimates for model 13, examining parameters influencing percentage body mass gains during foraging trips. Significant parameters are in bold. Italicized values for "year" are means for each category. 95% confidence intervals given in square brackets

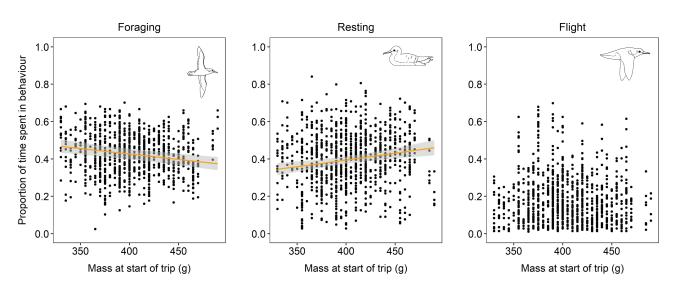| Parameter		Estimate/*mean*	χ2	P
Starting mass (g)		**−0.29 [−0.32, −0.25]**	**133.61**	**<0.0001**
Sex (male)		**6.68 [3.00, 10.38]**	**12.06**	**0.00052**
Trip duration		0.17 [−0.20, 0.56]	0.81	0.37
Prop foraging		−1.83 [−10.00, 6.93]	0.15	0.70
Year	*2015*	*12.99 [10.34, 15.64]*	6.71	0.08
	2016	*16.29 [12.18, 20.4]*		
	2018	*8.84 [3.31, 14.36]*		
	2019	*11.80 [9.50, 14.11]*		

FIGURE 5. Proportion of time during the foraging trip spent in each of foraging, rest, and flight behavior as a function of mass (g) at the beginning of the trip. Shaded areas indicate 95% confidence intervals of model-estimated regression. There was no relationship between the proportion of time spend in flight and body mass.

night, and because longer foraging trips can themselves be beneficial. Long trips can help birds to optimize the balance between commuting and foraging time, and so that they can exploit further distance foraging locations that are more productive than those closer to the colony (Dean et al. 2015, Shoji et al. 2015b). This relationship between body mass and foraging trip duration further explains the observed correlation between the duration of consecutive incubation shifts: birds that incubate for longer will need longer foraging trips to compensate, corresponding to a lengthened shift by the partner.

Egg neglect was infrequent, observed in just 8% of shifts over the entire study. The mass of a bird at the start of its incubation shift predicted the probability that the shift ended in neglect, with heavier birds being less likely to neglect. We found no support for a mass threshold for neglect, nor was there evidence of a relationship between incubation shift duration and the probability of neglect, suggesting this decision was not driven by incubating birds

being forced to wait on the nest when their partners spent excessively long durations at sea. Rather, the low starting mass of neglecting birds meant they had insufficient reserves to fast for the duration of the shift. When neglect occurred, mass predicted the amount of time the bird remained on the nest before leaving, with heavier birds sustaining a longer period of incubation before departing to sea. Despite the resistance of Manx Shearwater embryos to the temporary chilling (Matthews 1954), hatching success was a decelerating function of egg neglect, with the probability of hatching decreasing rapidly for up to 5 days of neglect, at which point nearly every neglect egg failed to hatch.

The importance of body mass in determining the probability of neglect may explain the finding that foraging birds appear to factor information about their partner's condition into their decisions. This may be driven by short-term considerations (can the partner sustain the next incubation shift), but parents might additionally act to improve,

TABLE 6. Test statistics for models 14/15/16, examining parameters affecting the proportion of time spent in foraging, resting, and flight behavior respectively. Significant parameters in bold. Italicized values for "year" are means for each category. Estimates are given on the logit scale with 95% confidence intervals in square brackets

Parameter	Foraging			Resting			Flight		
	Estimate	χ2	P	Estimate	χ2	P	Estimate	χ2	P
Start mass (g)	**−0.002 [−0.004, −0.001]**	**19.24**	**<0.0001**	**0.003 [0.001, 0.005]**	**17.19**	**<0.0001**	−0.0004 [−0.002, 0.002]	0.11	0.74
Sex (male)	0.08 [−0.04, 0.21]	0.21	0.65	−0.001 [−0.18, 0.15]	0.09	0.77	−0.08 [−0.27, 0.12]	0.16	0.69
Trip dur	−0.01 [−0.04, 0.002]	1.62	0.20	−0.01 [−0.05, 0.03]	0.04	0.85	0.04 [−0.01, 0.09]	2.03	0.15
Prop commute	0.22 [0.15, 0.24]	1.72	0.19	0.04 [−0.59, 0.67]	0.09	0.77	0.39 [−0.39, 1.16]	1.01	0.32
Year 2015	*0.37 [0.35, 0.39]*	**44.91**	**<0.0001**	*0.41 [0.38, 0.44]*	*7.83*	*0.05*	*0.21 [0.19, 0.23]*	*16.88*	*0.0007*
2016	*0.47 [0.43, 0.50]*			*0.39 [0.35, 0.44]*			*0.15 [0.13, 0.18]*		
2018	*0.43 [0.39, 0.47]*			*0.44 [0.38, 0.50]*			*0.14 [0.11, 0.17]*		
2019	*0.45 [0.43, 0.47]*			*0.38 [0.35, 0.40]*			*0.17 [0.15, 0.19]*		

Notes: start mass = bird mass (g) at beginning of foraging trip; sex = male or female; trip dur = foraging trip duration; prop commute = proportion of trip spent commuting.

probabilistically, their partner's long-term survival if there is a benefit to pairing with the same individual in multiple years (Griffith 2019). Previous evidence suggests that the foraging decisions of Manx Shearwaters are pre-planned, with birds on long trips being found considerably further from the colony than those on short trips on the first day at sea (Guilford et al. 2008).

Our finding that foraging birds mediate their trip durations based on the condition of their partner demonstrates evidence of a cooperative approach to incubation investment. This furthermore indicates that shearwaters may have a mechanism to exchange information between the two parents. As a key sexually-selected trait (Hunt et al. 2009), many animals exhibit signal-based indicators of body size, mostly vocal (Hall et al. 2013, Vannoni and McElligott 2008, Zhao et al. 2018). However, the possibility that animals may be able to exchange information about short-term within-individual changes to body mass has not been explored, and it is thus unclear how individuals can communicate effectively to this end. One potential opportunity arises during vocal duets between partners on their reunion at the nest. Gémard et al. (2019) found that the calls of male Blue Petrels and Antarctic Prions [*Pachyptila desolata*] carry information about morphological characteristics of the caller. Furthermore, in other biparentally-caring species, vocalizations signal need (Boucaud et al. 2016a), indicate readiness to take over incubation (Boucaud et al. 2016b, 2017), and are correlated with levels of coordination (Kavelaars et al. 2019). It has been previously proposed that a process of negotiation may allow parents to come to collaborative decisions about their care (Johnstone et al. 2014, Johnstone and Savage 2019). Manx Shearwater vocalizations might therefore contain information that allows parents to negotiate informed decisions about trip duration based on a consideration of their own and their partner's reserves.

While males were found to take a greater share in incubation, they did not differ from females in either the number of shifts they incubated for nor the duration of these shifts. This conflicts with earlier studies that found males took on longer incubation shifts (Short-tailed Shearwater, Carey 2011; Northern Giant Petrel [*Macronectes halli*], González-Solís et al. 2000; Manx Shearwater, Thompson 1987) but matches findings in other species (Cape Petrel, Weidinger 2008; Banded Stilt [*Cladorhynchus leucocephalus*], Pedler et al. 2016). Instead, this difference in contribution probably arises due to a combination of small differences between males and females, which accumulate over the incubation attempt, as well as shorter first incubation shifts of females. This latter finding is probably driven by the energetic deficit the female has incurred from building the egg, which at 15% of its body mass (Brooke 1990), is substantial, and has also been observed in the Laysan Albatross (*Phoebastria immutabilus*; Fisher 1971) and the Northern

Fulmar (*Fulmaris glacialis*; Hatch 1990). While males were heavier than females, both sexes experienced a similar daily decay in body mass over incubation, suggesting that the short-term resource costs of incubation shifts are comparable for the two sexes, as observed in Wandering Albatross (*Diomedea exulans*; Weimerskirch et al. 1995). Furthermore, both males and females were equally likely to neglect the egg and waited similar durations of time before doing so. The similar behavior of males and females, and the relatively small increased contribution of males, together suggest that the greater mass of males is probably not adaptive in incubation, and might instead be more important in pre-laying behaviors, such as securing and defending the nest, or during the chick-rearing period, during which time males provide 40–50% more food to the chicks (Hamer et al. 2006). Indeed, the mass of both sexes gradually increased over the course of the incubation period, which may help birds to ensure they have sufficient reserves for the energy-intense provisioning period ahead. This furthermore suggests that the cooperative approach to incubation exhibited by Manx Shearwaters effectively works to reduce sexual conflict, hence helping to stabilize biparental care (Chase 1980).

New pairs were more likely to neglect their eggs than experienced pairs, despite showing no significant differences in their mass change, shift durations, or hatching success, making it difficult to identify from where this difference arises. This failure to detect effects on other facets of behavior could reflect the fact that our method for assigning experience meant that all individuals in "new" nests had necessarily been observed breeding in the previous year with a different partner and therefore had at least one year of breeding experience. Our failure to find differences between new and experienced nests beyond the probability of neglect may therefore suggest that the previously reported positive effects of experience on breeding success for Manx Shearwaters (Brooke 1978, Harris 1966) are not due to the duration of the pair bond, but rather the experience or age of the individual parents. Further research is needed to disentangle the relative contributions of individual and pair experience on breeding behavior and success (Griggio and Hoi 2011, van de Pol et al. 2006).

We found significant effects of year on lay date, shift duration, mass at the beginning of incubation shifts, foraging gains, and foraging effort. While there was no consistent pattern in the distribution of these effects (e.g., in 2019, birds laid earlier, were lighter on average, and showed normal foraging gains), this probably reflects annual variation in at-sea resource availability. Disentangling the effects of environmental variation is important to understanding allocation decisions and parental coordination, as the environmental context in which care is provided can influence the fitness benefits of cooperation for pairs (AlRashidi et al. 2010) and therefore the degree to which parents may be

selected to coordinate at all (Ihle et al. 2019). Future work should examine environmental variables and relate these to incubation behavior, including foraging effort, incubation shift duration, and the probability of neglect. Furthermore, the use of alternative data loggers, such as GPS, could allow the collection of higher-resolution data on these metrics. This study used GLS to collect coarse measures of behavior, as these have not been reported to adversely affect shearwater behavior compared to untagged birds (Gillies et al. 2020). However, future miniaturization and reduction in cost of biologgers should allow these data to be collected without undue impact.

Overall, our results provide evidence that Manx Shearwaters employ cooperative approaches to determining their trip durations that account for the condition of both parents. While the decisions underlying foraging trip duration, and consequently the duration of incubation shifts, are primarily driven by the resource requirements of the foraging bird, they are mediated by its partner's condition. While our results do not support a threshold mass at which incubating birds neglect the egg following a protracted fast, we do find evidence that neglect might be driven by an inability to sustain incubation due to an insufficient starting mass. As such, the regulation of both partners' body mass is of key importance both to maximize breeding success from the current reproductive attempt, and to preserve long-term survival and investment. This approach to the problem of dividing care between parents can reduce sexual conflict by allowing both members of the pair to maximize the efficiency of their parent investment (Johnstone et al. 2014). Through this strategy, Manx Shearwaters can effectively preserve their long-term condition both in preparation for the ensuing chick provisioning period, and for future reproductive attempts.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

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Ethics statement: All methods and procedures adhere to ASAB/ABS Guidelines for the Use of Animals in Research, and were approved by the British Trust for Ornithology (BTO) Unconventional Methods Technical Panel (permit number C\5311) and by the Wildlife Trust for South and West Wales under the name of Prof. Tim Guilford. Ethical approval was received from the Local Ethical Review Process of the University of Oxford. This project holds Islands Conservation Advisory Committee (ICAC) approval. Handling time during ringing, weighing, and geolocator deployments was kept to a minimum; deployment and retrieval of geolocators were conducted in the field and did not normally exceed 5 min. Geolocators weighed 1.5 g and have been previously reported as having no detrimental effects on Manx Shearwater foraging behavior (Gillies et al. 2020).

Author contributions: N.G., O.P., S.B., and T.G. conceived the idea and designed the methods. N.G. and O.P. analyzed the data. All authors contributed to data collection and provided feedback on the manuscript.

Data depository: Analyses reported in this article can be reproduced using the data provided by Gillies et al. (2022).

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