1 **CARRY-OVER EFFECTS FROM BREEDING MODULATE THE ANNUAL**

2 **CYCLE OF A LONG-DISTANCE MIGRANT. AN EXPERIMENTAL**

3 **DEMONSTRATION**

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15

1   *Abstract.* Carry-over effects relate to events or processes that influence individual

2   performance in a subsequent season, but their occurrence in the annual cycle of migratory

3   avian taxa is seldom studied. We investigated if different levels of resource allocation to

4   reproduction may result in carry-over effects that change the timing and destination of

5   long-distance migration. We reduced the parental investment of Cory's shearwaters

6   *Calonectris diomedea* by removing their chick at an early stage. When compared to

7   individuals with greater parental investment (controls which raised chicks to close to

8   fledging), manipulated birds started most stages of migration sooner, and returned to the

9   colony earlier at the start of the following breeding season. Late arrival in the subsequent

10   nesting season increased the probability of skipping a breeding year. Manipulated males

11   were less likely to engage in long-distance migration, which supports the idea that partial

12   migration is condition dependent. Our study demonstrates experimentally that energetic

13   or time-dependent costs of reproduction may have an enduring impact on migration

14   schedule and on non-breeding geographical distribution of long-distance migrants, which

15   may also influence the ability to breed in the following season.

16

17   Keywords: Costs of reproduction, Partial migration, Cory's shearwater, *Calonectris*

18   *diomedea*

19

1   INTRODUCTION

2   Seasonal migrations produce redistributions of organisms over large spatial scales. These

3   migrants may carry with them impacts of events or processes that occurred in habitats far

4   removed in time and space (Harrison et al. 2011). Environmental conditions experienced

5   in distant wintering areas, for example, may have a profound influence on geographical

6   distribution and reproductive performance at the breeding grounds (Marra et al. 1998,

7   Studds et al. 2008), with implications for population structure and dynamics (Norris &

8   Taylor 2006, Studds et al. 2008). Similarly, given that allocating finite resources (such as

9   time or energy) to reproduction may reduce their availability for tasks related to self-

10   maintenance (Reznick 1985, Stearns 1992), the corollary is that events during breeding

11   may influence geographical distribution, behaviour and survival during the non-breeding

12   period. Unravelling such relationships is critical for the determination of the causes of

13   intra-population variability in migratory strategies (Newton 2008, Chapman et al. 2011)

14   and for our understanding of how events during the annual cycle affect individual fitness

15   and population processes.

16   Amongst the first results suggesting carry-over effects of breeding on migration

17   are those from a recent study of black-legged kittiwakes *Rissa tridactyla* that linked

18   breeding success or failure to contrasting geographical distributions in the non-breeding

19   season (Bogdanova et al. 2011). Another study of savannah sparrows *Passerculus*

20   *sandwichensis*, found that the timing of breeding events is an important influence on

21   migration departure date (Mitchell et al. 2012a). Thus far, however, studies of carry-over

22   effects on migrants have largely relied on observations and inferences from correlations.

23   Correlative data can provide crucial insights, but ultimately experiments are needed to

1 disentangle confounding effects such as those caused by consistent differences between

2 individuals in resource acquisition, which likely underlie differences in individual quality

3 (e.g. Mitchell et al. 2012b).

4   The timing of successive events in the annual cycle of migrants may have major

5 consequences for fitness (Kokko 1999, Newton 2008). For example, many birds are

6 believed to adopt a time-minimization migratory strategy, suggesting that early arrival at

7 nesting or non-breeding grounds may be important for fitness maximization (Alerstam

8 2011). Delays at one point of the annual cycle, whatever their causes, may affect

9 subsequent stages (Harrison et al. 2011, Stutchbury et al. 2011), potentially in a

10 sequential fashion resulting in what has been coined a "domino-effect" (Piersma 1987,

11 Lourenço et al. 2011). Accordingly, an individual that is late at an early stage of its

12 annual cycle may be unable to recover (in terms of its migratory or reproductive

13 schedules) from this delay for quite some time, and hence will suffer from mismatches

14 between actual and optimal timings until recovery from the carry-over effects.

15 Individuals may also be able to adhere to an ideal schedule at key points in their annual

16 cycle but, in doing so, have to suffer the repercussions, for example in terms of general

17 body condition, which may entail energetic costs at a later stage.

18   Carry-over effects from reproduction may potentially affect the choice of

19 wintering quarters by migrants through a variety of mechanisms. For example if

20 individuals in better body condition at the end of the breeding season are better able to

21 endure the hardships of winter within the breeding range, they may opt to be sedentary in

22 order to return to their breeding locality early and better compete for nesting sites or

23 mates (Kokko 1999, Chapman et al. 2011). Alternatively, individuals in better condition

1 may have more time or energy at their disposal to engage in long-distance movements

2 (Bogdanova et al. 2011).

3   Here we present the results of an experiment designed to test the hypothesis that

4 the allocation of resources to parental care modulates the subsequent migratory strategies

5 of a long-lived pelagic seabird, Cory's shearwater *Calonectris diomedea*. By

6 experimentally reducing parental investment, freeing individuals from reproductive duties

7 at an early stage, we investigate if breeding effort *per se* entails carry-over effects that are

8 apparent in the non-breeding season. Furthermore, because Cory's shearwaters often skip

9 breeding (Mougin et al. 1997), we check whether variation in migratory strategies caused

10 by past reproduction have repercussions during the next nesting season that contribute to

11 breeding deferral, which would imply that the allocation of resources to reproduction in

12 one season may negatively impact the subsequent attempt.

13

14   METHODS

15 This research took place at a large colony on Selvagem Grande (30º09´N, 15º52´W),

16 Portugal. Most Cory's shearwaters from this colony winter in the South Atlantic and a

17 small proportion remains in the North Atlantic (Catry et al. 2011). Arrival at the nesting

18 colonies takes place mostly in March, laying occurs from late May to early June, hatching

19 in the second half of July, and fledging in late October and early November. Only one

20 egg is laid per breeding attempt and there are no replacement clutches. To study

21 migratory movements, we used Mk7 and Mk19 geolocator data loggers (British Antarctic

22 Survey, Cambridge) attached to a leg-band for the duration of the annual cycle (see

23 Appendix A for details).

1

2 *Experimental manipulation*

3 In 2009 and 2010, just after hatching in late July and early August, we randomly selected

4 nests (5 in each year) where breeding failure was induced by removing the young chick.

5 These chicks were fostered to non-study pairs that were still incubating eggs well beyond

6 the predicted hatching date; these eggs were assumed to be infertile or the embryo had

7 died. In all cases, the translocated chicks were immediately adopted, brooded and fed by

8 the foster parents. Only 1 out of 10 translocated chicks did not survive till late September

9 when nest checks ceased. The biological parents of translocated chicks (a total of 20

10 individuals) were captured at the nest and fitted with a geolocator, which was recovered

11 in the following nesting season, as for other birds (Appendix A). Three individuals did

12 not return, or lost the geolocators, resulting in a sample of 17 manipulated individuals (of

13 which 14 formed mated pairs).

14   Timing of migration was compared between (i) experimental birds (with imposed

15 breeding failure), and (ii) controls (23 individuals that came back with functional

16 geolocators, only 2 forming a mated pair, out of a total of 30 deployments), which were

17 fitted with loggers in August and raised their chick at least until late September (and most

18 likely to fledging in late October) of the same year. Furthermore, experimental

19 individuals were also followed on a previous or subsequent breeding season when they

20 were left to raise their chick successfully. Thus, we had available both independent

21 controls (other birds) in the same season as the experiment, and self-referential controls

22 (same bird in a different season) to enable comparisons that account for possible

23 individual effects.

1   In order to assess if arrival date affects the subsequent probability of breeding, we

2   used an enlarged dataset, which included only observations from non-experimental birds

3   equipped with geolocators (51 individuals) from Selvagem Grande for the years 2008-

4   2010.

5

6   *Analyses*

7   Each individual bird contributed a single data point to analyses, with the exception of the

8   matched design where experimental individuals served as controls for themselves in

9   different years, and the analysis was of repeated measures. It could be argued that pair

10   members should not be considered independent in our analyses. However, members of

11   the pair migrate independently and preliminary tests did not indicate the existence of

12   correlations in phenology between partners. Furthermore, when the data were reanalysed

13   using males only the results remained significant (not shown). Hence, we opted to retain

14   individuals as independent observations in most analyses (but see below).

15   Possible sex and year effects on the dependent variables of interest were tested by

16   including those as predictors in generalised linear models with experimental status as an

17   independent variable. Sex and year never proved to be significant predictors of the

18   dependent variables and hence were not retained in the final models. This is in

19   accordance with previous evidence that timing of breeding and of migration in Cory's

20   shearwaters are little affected by sex and show limited annual variation (e.g. Dias et al.

21   2011).

22   As Cory's shearwaters from Selvagem Grande use up to 6 alternative wintering

23   areas (Dias et al. 2011), our sample sizes did not provide sufficient statistical power to

1 compare the overall wintering distributions of experimental and control birds. However,

2 we were able to compare the proportion of birds in each group that carried out a long-

3 distance migration *versus* the alternative strategy of remaining sedentary in the Canary

4 Current. This only applies to males, as female Cory's shearwaters from Selvagens only

5 exceptionally remain resident in the Canary Current.

6   Given the lack of replicates for most wintering areas, it was not possible to

7 include wintering region as a factor in analyses of the timing of movements. Hence, we

8 used two complementary approaches: we compared timing of movement irrespective of

9 choice of wintering area, as this still afforded useful biological insights, and furthermore

10 repeated these analyses including only the birds that used the main wintering area (the

11 Benguela Current – off Southern Africa).

12   When testing for the effects of the manipulations on breeding in the following

13 year, we only considered one (randomly selected) individual per nesting pair, as divorce

14 is rare in Cory's shearwaters and breeding decisions of (previous) mates are therefore not

15 usually independent. Sample sizes in different tests differed, amongst other reasons,

16 because the start date of the long-distance migration and of crossing the 10ºN parallel was

17 not relevant for individuals that were either sedentary or did not winter in the South

18 Atlantic.

19   Light data from geolocators were analysed with Transedit and Birdtracker

20 softwares. Statistical analyses were carried out using the software R.

21

22   RESULTS

23 *Non-breeding distribution*

1   Four out of the 7 experimental males (in which breeding failure was induced) stayed in

2   the Canary Current region over winter, whereas none of the 14 control males did so

3   (Fisher's Exact Test, P = 0.006, Fig. 1). No females of either group were resident.

4

5   *Phenology*

6   Birds that were induced to fail commenced their autumn (outward) migration sooner,

7   departed earlier from wintering areas at the start of the return migration, and returned to

8   the colony earlier than controls (Table 1). These results hold when considering only the

9   individuals that wintered in the Benguela Current, but it is interesting to note that there

10 was no significant difference between groups regarding the date of arrival at the

11 wintering grounds (Fig. 2).

12   Within-individual trends were similar to the above ones. After induced breeding

13 failure, individuals departed 20.2 ± 24.0 days (n=11) earlier than they did in a year when

14 they were successful (GLMM: Manipulation effect: F = 7.83, P = 0.019, Year effect: non-

15 significant) and the following season they arrived back at the colony 8.7 ± 16.0 days

16 (n=15) earlier than they did after a successful breeding season (GLMM, F = 5.2, P =

17 0.039).

18

19 *Probability of nesting in subsequent season*

20 Including a single, independent representative from each pair, all 10 (100%) manipulated

21 birds that returned to the colony nested in the subsequent season, compared with only 14

22 (64%) of 22 controls (Fisher's Exact Test: P = 0.035). Amongst non-manipulated

23 individuals, the date of arrival at the colony was a significant predictor of the probability

1 that a bird would attempt to breed (Generalized Linear Model; χ^2_1 = 4.7, n = 51, P =

2 0.030; see Appendix B).

3

4   DISCUSSION

5 The present study demonstrated experimentally that the level of parental investment in

6 one season conditions the subsequent migratory strategy and schedule, with carry-over

7 effects that extend into the following breeding season. Previous studies have shown that

8 during the late nesting season, Cory's shearwaters that experience a breeding failure use

9 the discretionary time and energy at their disposal to begin the annual moult of flight

10 feathers sooner than successful breeders (Alonso et al. 2009). Hence, once freed from

11 reproduction individuals are able to allocate more resources to self-maintenance, which

12 may release them from constraints that more stringently limit the migration strategies of

13 the birds that raise a chick to fledging.

14   That individuals that failed reproduction early were able to migrate first is perhaps

15 no surprise (e.g. Mitchell et al. 2011a). However, late departure *per se* did not result in a

16 sequential chain of delays for the migrating birds, because successful birds were not late

17 when arriving at the main wintering grounds (Fig. 2), i.e., there was no evidence of a

18 simple "domino-effect".

19   Shearwaters are not territorial at sea and there may be no advantage in arriving

20 earlier than potential competitors at wintering sites (Kokko 1999). In contrast, state-

21 dependent arrival at nesting grounds is expected when there is a strong competition for

22 nesting sites (Kokko 1999), which does apply to Cory's shearwaters (Ramos et al. 1997).

23 Hence, assuming that failed breeders would be in a more favourable state because of their

1   reduced parental investment, we would expect manipulated birds to have higher capacity

2   for an earlier return to the colony for the next breeding attempt, even though they did not

3   arrive earlier at the winter quarters. Actually, this is exactly what we observed. Failed

4   birds departed earlier from wintering areas and arrived sooner at the nesting colony.

5   Other failed breeders simply forewent migration altogether and remained in the region of

6   the nesting colony throughout the winter, which again left them in a better position for

7   early return. The importance of an early arrival at the nesting grounds was confirmed by

8   its influence on the probability of subsequent breeding. This mechanism would explain

9   why successful breeders were less likely to nest in the following year than manipulated

10   birds, which is clearly a major cost of full reproductive allocation.

11   Protandry is not known in Cory's shearwaters (Dias et al. 2011) and sex had no

12   apparent influence on the timing of migration in our analyses. Furthermore, the repeated

13   migrations by the same individuals with contrasting breeding outcomes in different years

14   confirm that most of the patterns reported here were caused neither by sex nor by any

15   other fixed individual traits (either genetic or phenotypic).

16   Cory's shearwaters from our study population are clearly partial migrants; some

17   individuals stayed in the region of the colony year-round, while others moved several

18   thousand kilometres away. Partial migration is a complex phenomenon, with most

19   available evidence suggesting it is condition-dependent rather than under strict genetic

20   control (Chapman et al. 2011). Our experimental evidence supports this conclusion and

21   the predictions of a game-theoretic model indicating that strong competition for nesting

22   territories or sites may lead to partial migration and that it is the birds in better condition

23   that should remain resident (Kokko 1999). The ability to experimentally influence the

1 decision of staying or going in a long-distance migrant by manipulating its breeding

2 effort potentially opens a range of possibilities for the study of partial migration and of

3 behavioural and physiological adaptations to migration and residency. That breeding

4 outcome can have a major influence on the non-breeding geographical distribution of

5 individuals (Bogdanova et al. 2011, this study) may have considerable implications in the

6 way we think about various aspects of bird migration, from its evolution to the applied

7 aspects linked with the conservation biology of migratory species.

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1   ECOLOGICAL ARCHIVES

2   Appendix A. Tracking methods and analysis of movement data.

3   Appendix B. Supplementary figure depicting the relationship between the date of the first

4   arrival at the nest and the probability of breeding in the same season.

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1 Table 1. Differences in migration schedule and nest attendance by manipulated (early

2 failure) and control (successful) individuals. Sex and year effects, and interactions with

3 other variables, were non-significant; hence, only experimental status was retained in the

4 GLM models. Values are means ± SD, with sample sizes in parentheses.

Variable	Manipulated	Control	F	P
Departure from colony	10 Oct ±28d (13)	9 Nov (±20) (23)	15.3	**<0.0001**
Departure long-distance migration	20 Oct ±27d (13)	13 Nov (±20) (23)	9.3	**0.007**
Crossing of 10ºN parallel	15 Nov ±08d (13)	25 Nov (±17) (20)	3.8	0.060
Arrival at wintering area	06 Dec ±13d (13)	09 Dec (±21) (23)	0.2	0.632
Departure from wintering area	14 Feb ±05d (13)	23 Feb (±10) (23)	10.0	**0.003**
First return to colony	10 Mar ±15d (17)	29 Mar (±28) (23)	6.3	**0.016**

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6

1   Fig. 1. Winter distribution of control (successful breeders – left panel – 14 individuals)

2   and manipulated (early failure – right panel – 7 individuals) male Cory's shearwaters

3   given by geolocator positions. Each colour represents one individual. Red cross indicates

4   colony location (Selvagens). The proportion of individuals that stayed in the Canary

5   Current (around colony) *versus* those that moved to distant wintering locations differed

6   significantly between the experimental groups (Fisher's Exact Test P = 0.006).

7

8

9   Fig. 2. Comparisons of the migration schedules of manipulated (early failure – shaded

10   grey) and control (successful - unshaded) Cory's shearwaters that wintered in the

11   Benguela Current region. Milestones include: departure from the nesting colony; crossing

12   of the 10ºN parallel in autumn; arrival at the wintering area (Benguela Current); departure

13   from the wintering area; arrival at the nest site. Differences in departure from the colony

14   (F = 8.2, P = 0.009), departure from Benguela (F = 9.2, P = 0.006) and arrival at the

15   colony (F = 4.6, P = 0.043) between manipulated birds and controls are statistically

16   significant, but differences regarding the crossing of 10º N and of arrival at Benguela

17   Current are not (respectively, F = 1.0, P = 0.43 and F = 0.3, P = 0.56).

APPENDIX A

Tracking methods and analysis of movement data

To study migratory movements of Cory's shearwaters, we used Mk7 and Mk19

Geolocator data loggers attached to a leg-band for the duration of the annual cycle.

Geolocators were deployed on the study birds around hatching or during the chick-

rearing period and recovered on the following breeding season. Loggers only weigh 0.5%

of the body mass of the adult Cory's shearwaters and are not known to have a significant

impact on their condition or behaviour (Dias et al. 2012). Loggers record light levels,

from which we estimated the sunset and sunrise times and then the positions of each bird

twice a day (one at local midday and other at local midnight), with an accuracy of

approximately 186 ± 114 km (Phillips et al. 2004). Light data were analysed with

Transedit and Birdtrack software, assuming a sun elevation angle of -4.5 degrees (based

on ground-truthing of loggers carried out before and after deployment). Unrealistic

positions (those resulting from interference in light data at dawn or dusk, or around

equinox periods) were removed from the analyses.

The timing of two key events related to post-breeding departure were extracted

from the geolocator data. "Departure from the colony" was the day after the last date that

the bird was < 300km from the nest (although in some cases, these birds migrated no

further than the Canary current region), whereas "departure for long-distance migration"

was the date when the bird started directed movement towards a distant (> 2000 km)

stopover or wintering area. We also used the crossing of the 10ºN parallel as a clear

"landmark" for the migration into the South Atlantic. The same could not be used during

the return migration in spring due to the disrupting effect of the equinox on the ability to

determine latitude. However, Cory's shearwater nests are in burrows or caves and their diurnal attendance of such shaded places can be detected readily by analysing light levels recorded by the loggers. It was therefore possible to determine the date of first return to the colony.

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APPENDIX B

Fig. B1. Relationship between the date of the first arrival at the nest and the probability of breeding in the same season in previously successful Cory's shearwaters (Generalized Linear Model; $\chi^2_1 = 4.7$, n = 51, P = 0.030).