Outflying climate change

Optimal timing of migratory geese breeding in a warming Arctic

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CHAPTER 4

Effects of harness-attached tracking devices on survival, migration, and reproduction in three species of migratory waterfowl

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ABSTRACT

Tracking devices have enabled researchers to study unique aspects of behavior of birds. However, it has become clear that attaching these devices to birds often affect their survival and behavior. While most studies focus on negative effects on return rates only, it is essential to measure potential negative effects of tracking device attachment on the full range of behavioral aspects of birds, as tracking devices can affect the studied behavior. At the same time we should aim to improve our current methods to reduce these effects. We used a modified harness attachment to attach tracking devices to a total of 111 individuals of three goose species (Greater White-fronted Geese, Brent Geese, and Barnacle Geese) to study their migratory behavior. By creating control groups of birds marked with color bands, geolocators and/or neck collars, we were able to compare return rates, body condition, and migratory and reproductive behavior, thus allowing a much broader comparison than return rates alone. Birds with harness-attached tracking devices had lower return rates, which can partly be explained by increased rate of divorces, but is likely also the result of reduced survival induced by the harness attachment. This effect differed between species and sexes. A comparison of Barnacle Geese equipped with tracking devices and with geolocators on color rings, showed that birds equipped with tracking devices were only slightly delayed in timing of migration and reproduction, and otherwise were not affected in reproductive output. We thus argue that tracking devices can be used for studies on migration timing. Nevertheless, given the effect of tracking devices on survival and divorce rate which differed between sexes and species, we stress that researchers should carefully consider which birds to tag in order to reduce potential negative effects.

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Introduction

With the rise of advanced electronic tracking devices, such as satellite transmitters and GPS-loggers, scientists have become able to gather detailed data on movement of birds, allowing unique insights in their ecology and behavior (Seegar et al. 1996; Kays et al. 2015). At the same time it has become clear that attaching tracking devices to birds can potentially harm them or affect their behavior or survival (Barron et al. 2010), and the recorded data of tracking devices may thus be influenced by the tracking device itself. However, there are only limited means to test for these potential negative effects, as tracking devices in most cases provide the only approach to gather data on movement of animals. To ensure that tracking data actually reflects the natural behavior of birds, it thus becomes important to find ways how to test for potential effects of tracking devices, and to develop attachment methods which have the least amount of negative effects.

Due to the possibility of attaching solar-powered tracking devices which make use of GPS, and the small chance of the bird losing the device over a longer time period, harness attachments are the most common attachment method for larger birds, including raptors (Klaassen et al. 2008b; Vansteelant et al. 2015) and waterfowl (Gladher et al. 1997; Lameris & Kleyheeg 2017). However, harness attachments often have negative effects on birds, including reduced survival rates and reproductive success (Ward and Flint 1995; Garrettson & Rohwer 1998), reduced migratory flight speed (Hupp et al. 2015), and changes in behavior (Glahder et al. 1997). Although many studies report on negative effects of harness attachment on a single behavioral aspect, only a few studies make an attempt to study all potential negative effects together (but see Hupp et al. 2006), thus showing the full extent of potential negative effects. Most notably, negative effects on migration are difficult to study as tracking devices often form the only approach to measure this for individual birds, and hence these effects have hardly been studied (Barron et al. 2010). It is however important to study effects on multiple behavioral aspects, as negative effects can also carry over across parts of the annual cycle. As an example, timing of migration can be strongly linked to timing of reproduction, and relatively small effects early in the season can thus ultimately affect the fitness of a bird.

Some of the negative effects of harness-attached tracking devices seem related to the harness attachment itself. Because migratory birds vary in body mass during the year (Ankney 1982), harnesses may become too tight or too loose, which can cause irritation for the bird (Chan et al. 2016) and abrasian of the skin (Cappelle et al. 2011). The type of harness and the way the harness fits the individual bird can be decisive for reducing the influence on the bird (Chan et al. 2016) and thus how representative the tracking data are for normal behavior (Wilson and McMahon 2006).

We thus aimed to improve an existing harness design to fit individual birds, and to examine the potential negative effects of this harness attachment for a set of behavioral
aspects, including survival, migration, and reproduction, in order to gain a complete overview of the potential negative effects of this harness attachment. We used the harness to attach tracking devices to three Arctic-nesting migratory species of geese, including Greater White-fronted Geese Anser albifrons, Brent Geese Branta bernicla, and Barnacle Geese Branta leucopsis. We additionally created control groups of birds equipped with color bands and neck collars, including color bands with attached geolocators to record migration timing, and compared effect sizes between tagged birds and their control groups for survival, timing of migration and reproduction and reproductive output.

**Methods**

We modified an existing full-body harness design (e.g. Klaassen et al. 2008b) with a neck and body loop (Figure 4.1). Straps consisted of three materials (Teflon, Tygon, and nylon) to create a sturdy, but smooth, harness that was tubular in shape. We included sliding copper rings so we could quickly adjust the size of the neck and body loops when fitting the harness on different birds, and which can be squeezed tight with pliers to fix the size of the loops. Stainless steel rings were used to connect the harness to the tracking device. Harnesses can be made to fit different-sized species by adjusting the length of the straps. Full methods and instructions on how to construct and deploy the harness can be found in Lameris et al. (2017a).

**Study species and capture methods**

From 2012 to 2014 we equipped in total 111 geese with tracking devices and the harness we developed. Apart from a tracking device, all birds received metal and color bands for identification in the field. A larger sample of birds caught in a similar fashion as those equipped with tracking devices was equipped with colour bands or neck bands.

During the winters of 2013/2014 and 2014/2015 in Noord Brabant, The Netherlands, 35 Greater White-fronted Geese (7 males, 7 females, 21 juveniles) were caught in family groups using a remote controlled clap net (see Kölzsch et al. 2016a). Each bird was equipped with a plastic, numbered neck band and a 45-g e-obs GPS-GSM transmitter with the described harness. Another 92 birds were captured and equipped only with neck bands.

In April and May 2012 on the islands Terschelling and Schiermonnikoog, The Netherlands, Brent Geese were caught using canon nets and 30 male geese (21 on Terschelling, 9 on Schiermonnikoog) were equipped with plastic, numbered color bands and 16 g UvA-BiTS GPS-loggers (Bouten et al. 2012) with a prototype of the harness, while a control group was equipped with color bands only. The prototype differed from the later type by lacking the outer layer of Teflon and having attachment rings made of carbon steel instead of stainless steel. In 2014 Brent Geese were caught using canon nets
on Terschelling, and 6 female Brent Geese were equipped with 19 g UvA-BiTS GPS-loggers and the standard version of the harness (as described above: including an outer layer of Telfon and with attachment rings made of stainless steel). For our analysis on return rates, only geese caught on Terschelling were used as observation effort on Schiermonnikoog was too low.

Figure 4.1: Schematic design of the harness attachment design and study species. (A) a schematic design of the harness attachment design with locations indicated where cramping rings are placed. Before deployment the harness is attached to the front end of the tracking device (upper picture). During deployment the harness is fastened on the goose by placing the neck loop over the head and attaching the ends of the body loop to the sides of the tracking device (under the wing of the bird). The cramping rings are used to adjust the size of the harness to fit the individual bird. (B-D) The study species equipped with tracking devices and the harness: (B) a male Brent Goose; (C) a family Greater White-fronted Geese and (C) a female Barnacle Goose.

In June and July 2014 at the Kolokolkova Bay, Russia, 40 adult female Barnacle Geese were caught on the nest during incubation using a remote controlled clap net, and equipped with plastic color band and 19 g GPS-loggers (UvA-BiTS, Bouten et al. 2012) with the described harness. A control group of 40 adult female geese was caught on the nest (22
birds) and by rounding up flightless geese during molt (18 birds), and equipped with two plastic color bands (6.6 g total) and an Intigeo C-65 Migrate Tech geolocator (1 g) attached to the left color band. Because the geolocator weighed only a small fraction of the total weight of the two color bands, we assume that geese equipped with color rings and a geolocator would not differ in any behavior from geese with only color bands. As some of the geese in the control group were caught during catches during the molt period rather than on the nest, we ran analyses separate for the complete control group (40 geese) and the subset of geese caught on the nest (22 geese; thus in similar state as the geese with GPS-loggers).

Comparison of parameters

To calculate one-year return rates we collected all resighting data from the focal birds from www.geese.org, an online platform where observers can submit sightings of individually marked geese and swans. Observations from volunteer ring reads as well as those made by the researchers themselves were included. For Barnacle Geese, we calculated return rates based on birds caught during the molting period one year after equipping the birds with transmitters, as resightings of birds with GPS-loggers was biased, as we used GPS tracking

We compared the timing of departure and migration speed of Barnacle Geese with harness attachments and those with geolocators as a control group. UvA-BiTS GPS-loggers stored 48 to 288 accurate GPS locations (mean stationary error = 3.23 m, Bouten et al. 2012) per day. Geolocators are less accurate (error of 1.4 – 4.0 10³ km, Lisovski et al., 2012) and can be used to calculate a maximum of two longitude positions per day. The Intigeo C-65 geolocators recorded light intensity every 5 min. Data were retrieved at our study site in the Kolokolkova Bay, Russia, in the summer of 2015. Data from GPS-loggers were downloaded remotely using a Zigbee two-way receiver unit in the tracker that made connection to a UvA-BiTS base station and six relays (Bouten et al. 2012). Geolocators were retrieved from shot birds or by rounding up flightless birds during the molting period. Data from GPS-loggers were downloaded from the UvA-BiTS database as text files with latitude and longitude positions. After retrieving geolocators, data were downloaded and processed using the program Intiproc (Migrate technology 2014). Further analysis was carried out using the package ‘GeoLight’ (Lisovski & Hahn 2012) in R 3.1 (R Core Team). Twilight events were identified using the ‘threshold method’ (Ekstrom 2004) at a light intensity value of 2 (Lisovski et al. 2012) and used to calculate two longitude positions per day. For both spring migration tracks acquired using GPS-loggers and geolocators we determined the moment of departure from wintering site in the Wadden Sea area (first position with longitude > 9°) and the moment of departure from the Baltic Sea region (first position with longitude > 30°). For geese that did not stop in the Baltic Sea region and migrated continuously after departure from the Wadden Sea, the latter position
was often absent in geolocator data as these geese quickly arrived in the region north of
the Baltic Sea, which is governed by 24 hours of daylight during this period of the year.
For these geese, we took the day after the last day at which we could obtain a longitude
position as the day of leaving the Baltic region. We calculated the speed of migration as
the number of days in between departure from the wintering grounds and departure from
the Baltic region.

We measured reproductive performance of Barnacle Geese with harness attachments
and those with geolocators at our study site at Kolokolkova Bay, Russia (van der Jeugd
2003). We searched for new nests and checked known nests every 2 to 3 days between 31
May and 25 June 2015. Eggs were marked and number of eggs was recorded at every visit.
Nest initiation dates were determined as the day the first egg was laid. For incomplete
clutches found during egg laying, initiation date was estimated as follows: 1 egg, day of
discovery; 2 eggs, day of discovery minus 1; 3 eggs, day of discovery minus 3, 4 eggs, day
discovery minus 4 (van der Jeugd et al. 2009). Clutch size was only determined for
nests with the same number of eggs after more than two visits. We measured reproductive
performance of Brent Geese with harness attachments by observing them on their
wintering grounds in the Wadden Sea, the Netherlands, and noting whether they were
accompanied by juveniles.

In July and August 2015, we captured flightless Barnacle Geese using herders and
boats. We visually assessed condition and damage on geese carrying harness attachments.
We weighed geese using a spring scale (± 10 g).

Statistical analyses
All analyses were conducted using R 3.0.2 (R Development Core Team 2014). We
compared one-year return rates of birds with the harness attachment and the control
groups. We tested for significant differences between return rates using binomial logistic
regression models that included species, sex, experimental group (harness or control),
and the interaction effect of experimental group and species / sex. We used one-tailed
Mann-Whitney U tests to compare departure date from the wintering grounds, departure
date from the Baltic Sea region, migration speed, nest-initiation dates, and clutch sizes of
Barnacle Geese equipped with harness attachments and their control group, which were
either geese with geolocators or birds without attached devices (i.e., only color bands).
For some comparisons, sample sizes were low, and smaller effects of harness attachments
were probably not detectable. Therefore we provided 95% confidence intervals of effect
sizes (Cohen’s D) for all tests, rather than conducting a post-hoc power analysis (Colgrave
& Ruxton 2003).
Results

Return rates
Geese with tracking devices experienced reduced one year return rates compared to their control group (Attachment coefficient = -1.14 ± 0.28 (SD), z = -4.0, P < 0.001, Table 4.1). This did not differ between species and sexes, as the interaction effect between attachment and species/sex was not present in the highest ranking models (Table 4.2).

Migratory behavior
We found no significant differences in the migratory behavior of Barnacle Geese with harness-attached GPS-loggers and those with geolocators. However, the effect size suggests that birds with GPS-loggers were potentially slightly delayed (-1 day) in moment of departure, including the moment of departure from the Wadden Sea region (GPS-logger, N=18: 45 ± 6; geolocator, N = 18: 43 ± 10 days since 1 April; W = 136, d = 0.43, 95% CI [-0.26, 1.11], P = 0.21) and the moment of departure from the Baltic Sea region (GPS-logger, N=18: 50 ± 3; geolocator, N=19: 48 ± 3 days since 1 April; W = 138.5, d = 0.47, 95% CI [-0.21, 1.15], P = 0.16). There was no difference in migration speed (GPS-logger, N = 18: 4.55 ± 4.60; geolocator, N=18: 5.33 ± 7.84 days; W = 162, d = 0.22, 95% CI [-0.46, 0.90], P = 0.51).

Reproduction
We found that 27 of 40 Barnacle Geese with harness-attached GPS-loggers returned to breed in 2015 and 20 initiated nests (17 nested successfully). Barnacle Geese with geolocators also bred successfully, based on 12 found nests out of 40 tagged birds. Clutch sizes of geese with GPS-loggers did not differ from those of either geese with geolocators or other birds in the colony (GPS-logger: 4.3 ± 1.0 eggs, N = 18; geolocator: 4.5 ± 0.93 eggs, N = 11; colony: 4.4 ± 1.2 eggs; N = 351; GPS-logger vs geolocator: W = 80, d = 0.51, 95% CI [-0.28, 1.31], P = 0.19; GPS-logger vs colony: W = 3307, d = 0.51, 95% CI [-0.36, 0.59], P = 0.64). However, geese with GPS-loggers started laying their eggs on average 2 - 3 days later than geese with geolocators and other geese in the colony (GPS-loggers: 37.1 ± 1.9 days since 1 May, N = 18; geolocator: 34.1 ± 2.0 days since 1 May, N = 8; colony: 34.7 ± 2.4 days since May 1st, N = 216; GPS-logger vs geolocator: W = 106.5, d = 1.35, 95% CI [0.39, 2.31], P = 0.004; GPS-logger vs colony: W = 917.5, d = 0.67, 95% CI [0.18, 1.16], P < 0.001).

Of the female Brent Geese equipped with harness attachments, three of five females that returned to the wintering grounds in 2014 nested successfully, as they were accompanied by juveniles. Tagged males did not nest successfully in 2013, but it must be noted that this was a year with generally very low nesting success, also for untagged geese.
Table 4.1: Return rates of birds equipped with harness-attached tracking devices (tagged birds) compared to their control groups, equipped with color bands or neck collars. For each return rate, the time frame of measurement is given over which the return rate has been measured, and the coefficient value taken from logistic regression models, representing the change in log odds.

<table>
<thead>
<tr>
<th>Species</th>
<th>Time frame of measurement</th>
<th>Sample size tagged birds</th>
<th>Return rate</th>
<th>Sample size control group</th>
<th>Return rate</th>
<th>Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brent goose (males)</td>
<td>May 2012 – May 2013</td>
<td>21</td>
<td>0.52</td>
<td>37</td>
<td>0.78</td>
<td>-0.81</td>
</tr>
<tr>
<td>Brent goose (females)</td>
<td>May 2014 – May 2015</td>
<td>6</td>
<td>0.83</td>
<td>15</td>
<td>0.93</td>
<td>-0.65</td>
</tr>
<tr>
<td>Barnacle goose (females)</td>
<td>June 2014 – August 2015</td>
<td>40</td>
<td>0.45</td>
<td>40</td>
<td>0.55</td>
<td>-0.40</td>
</tr>
</tbody>
</table>

1 For this comparison only the subset of control birds caught on the nest is used as a control group

Table 4.2: Final binomial logistic regression models for return rates over species (S), sex and age groups (A), attachment treatment (T), the interaction between treatment and species (T*S) and the interaction between treatment and sex and age groups (T*A). Coefficient values are given, with asterisks denoting significant effects (p < 0.05: *; p < 0.01: **; p < 0.001: ***).

<table>
<thead>
<tr>
<th>Return rate</th>
<th>Intercept</th>
<th>Species (S)</th>
<th>Sex/Age (A)</th>
<th>Treatment (T)</th>
<th>Treatment* Species (T*S)</th>
<th>Treatment* Sex/Age (T*A)</th>
<th>Degrees of freedom</th>
</tr>
</thead>
<tbody>
<tr>
<td>~ S + T</td>
<td>0.673</td>
<td>0.88*</td>
<td></td>
<td></td>
<td>-1.14***</td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>~ T</td>
<td>0.900</td>
<td></td>
<td></td>
<td></td>
<td>-1.14***</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>~ S + T + T*S</td>
<td>0.82</td>
<td>1.38*</td>
<td></td>
<td></td>
<td>-0.38</td>
<td>-1.17</td>
<td>6</td>
</tr>
<tr>
<td>~ S</td>
<td>-0.065</td>
<td>1.15**</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>~ S + A + T</td>
<td>0.669</td>
<td>1.36*</td>
<td>-0.64</td>
<td>-1.13***</td>
<td></td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>~ S + T + S*A</td>
<td>0.395</td>
<td>1.47**</td>
<td></td>
<td>-0.71</td>
<td>-1.04</td>
<td></td>
<td>8</td>
</tr>
</tbody>
</table>
Other effects

For the 18 Barnacle Geese with harness-attached GPS-loggers which we recaptured during molt, we were able to assess physical damage on the geese caused by the harness, as well as overall condition and weight of the bird. Of 18 geese, 12 were either not damaged, missing some down feathers in the armpits or had some broken back feathers below the logger. Four geese had both slightly damaged armpits and broken back feathers and two birds had suffered from more severe damage, showing old wounds in one or both of the armpits. Body mass during molt did not differ between birds with GPS-loggers, geolocators or only color-rings (GPS-marker: 1621 ± 120 g, N = 18; geolocator: 1645 ± 103 g, N = 22; color-bands: 1620 ± 137 g; N = 3186; GPS-marker vs geolocator: W = 237, d = 0.34, 95% CI [-0.31, 0.99], P = 0.29; GPS-marker vs colony: W = 1720, d = 0.05, 95% CI [-0.44, 0.53], P = 0.85). The harnesses themselves were only slightly damaged and showed some wear of Teflon at the outer loops.

Although all 14 observed male Brent Geese with harness-attached tracking devices had a mate after the initial catch in 2012, only 36% of those males returned with their original partner in 2013 (but at least two males were able to find a new partner during that spring period). Of the six females with harness-attached tracking devices in 2014, all returned with their mate.

Of seven families of White-fronted Geese equipped with harness-attached tracking devices, the parents of two families separated within a week after tag attachment. Only one of the six tagged juveniles in those two families was not shot or predated during spring migration. Even if juvenile survival was higher for the five other families, none of the parents of those families returned to the wintering grounds together in the following year.

Discussion

We show that harness-attached tracking devices can have negative effects on return rates and some behavioral aspects, but effects can also importantly differ between species and sexes. Reduced return rates of geese with harness attachment compared to a control group can be partly explained by birds not returning to their original wintering or breeding grounds, but we argue that this is largely the result of a reduced survival. In addition we show that tracking devices can affect behavioral aspects, including an increased probability of divorcees, but only slightly affect timing of migration and reproduction.

Return rates can be used as an index for survival, if individuals have high site fidelity and a high probability of being observed if alive. Individual Brent Geese return to the island of Terschelling every spring, and due to the open landscape and high observation effort, individuals have close to a 100% chance of being observed when alive. The same holds for Greater White-fronted Geese, due to the good visibility of the neck collars.
combined with a good network of voluntary ring-readers in the Netherlands. We observed female Barnacle Geese at their breeding colony, to which female geese are known to return to every year (Karagicheva et al. 2011), and we maximized our observation and recapture effort in an attempt to detect all individuals present. Non-observed individuals were never detected in subsequent years, supporting the conclusion that detection rate was high and non-observed individuals were likely dead. Lower return rates should thus indeed represent lower survival rates.

However, male geese tend to follow the female year-round, and can thus change wintering area when divorcing their original partner. Divorce rates are however extremely low for geese (average of 3% per year for several species of geese) because they benefit from long-lasting partnerships (Ens et al. 1996). We found that divorce rates for male Brent Geese and Greater White-fronted Geese with harness-attached tracking devices were unexpectedly high, and increased divorce rates have also been reported for female Brent Geese with transmitters (Ward & Flint 1995) and neck collars (Lensink 1968). Attachment of a tracking device might affect the quality of the bird as a partner, driving divorces between birds. Other studies on Brent Geese equipped with harnesses indeed find birds to be of lower quality, as these birds experienced relatively low reproductive success and it is suggested that pairs where one of the birds is tagged forego breeding (Green et al. 2002; Clausen et al. 2003). After a divorce, birds can suffer from reduced reproductive output as they more often seem to mate with younger, inexperienced partners (Leach & Sedinger 2016) and birds are less likely to survive while being divorced (Nicolai et al. 2012). The decreased return rates of male Brent Geese could also be affected by them going to different wintering sites, as divorced birds would follow their new partners to other wintering sites. Negative effects related to divorces could be sex-specific, as we find high divorce rates for male Brent Geese but not for female Brent or Barnacle goose. These effects of tracking device attachment could potentially be avoided when tagging females rather than males, and the choice of which birds are being tagged can thus importantly influence the success of a tracking study.

Besides potential shifts in wintering grounds for divorced male geese, decreased return rates of individuals equipped with harness-attached tracking devices likely indicate a lower survival of these birds. Some studies found harnesses to negatively affect return rates and survival in geese (Ward & Flint 1995; Dzus & Clark 1996; Garrettson & Rohwer 1998), but other studies did not find such negative effects (Fox et al. 2003; Fleskes 2003). These latter studies measured return rates over a shorter time span. An idea about additional causes of death from geese equipped with harness attachments could be gained from the Greater White-fronted Geese in this study, of which out of 35 birds, 14 had been retrieved as shot and 7 as predated by large birds of prey or fox during the spring migration following tag deployment. The increased susceptibility of bird with attached tracking devices to being predated or shot, can potentially be attributed to changes in
behavior, notably an increasing time spent preening (Enstipp et al. 2005). In addition, we expect that the cross-sectional profile of a backpack tag can change flight aerodynamics, causing additional drag during flight (Bowlin et al. 2010). This could negatively influence maneuverability or cause it to fly in the back of the flock, thus making it an easier target for hunters and predators. Although our study found negative effects on return rates, our survival rates of tagged individuals was definitively higher than in some other studies (Ward & Flint 1995).

Because harness attachments have a negative effect on survival, they likely also have non-lethal effects on migratory birds. By using a control group from which we have individual data on migration timing gained from geolocators, we can convincingly show that harness attachments cause only a slight delay in timing of migration departure for Barnacle Geese. This effect was not significant and there exists a high degree of variation between individuals. At the same time, the migration speed of these birds was not affected. For comparison, an earlier study in Northern Pintails *Anas acuta* found that birds with harness-attached tracking devices arrived 19 days later on the breeding grounds in comparison to the population mean (Hupp et al. 2015). This is ascribed to a higher cost of migration, which is also suggested by models from Pennycuick et al. (2012). Also, we found a 2-3 day delay in laying date for Barnacle Geese with harness attachments, which is slight in comparison with earlier studies on Mallards *Anas platyrhynchos* with harness attachments, which were delayed between 8 – 14 days (Pietz et al. 1993; Rotella et al. 1993). Also, we do not find effects on clutch size nor on nest success, aspects of reproduction which are susceptible to negative effects of harnesses attachment (Pietz et al. 1993; Rotella et al. 1993; Garbettson & Rohwer 1998). Although we were not able to measure differences in body stores at arrival, any potential differences had disappeared after the nesting period because we did not find a difference in body mass of female Barnacle Geese with harness attachment and females in control groups.

Our results are concurrent with recent reviews on the negative effects of tracking devices on birds (White et al. 2013; Barron et al. 2010), and show that harness-attached transmitters can negatively affect survival but also pair-bonding, and thus the potential of birds to initiate breeding. These negative effects can have important consequences for behavior measured by tracking devices. On the other hand we find that although tracking device attachment does delay timing of reproduction, and possibly timing of migration, the delay is only slight, and other aspects of reproduction are not affected. In contrast with earlier studies which show strong negative effects on migration timing and reproduction for birds equipped with tracking devices (Hupp et al. 2015; Pietz et al. 1993; Rotella et al. 1993), we find that tracking devices are reliable tools to study timing of migration and reproduction. However, given our different results for different sexes, we stress that researchers make a good consideration which birds they equip with tracking devices.
Chapter 4

Acknowledgements

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