The effect of telemetric devices on the flight and swimming performance of birds

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Abstract

In studying animal behavior the use of telemetric devices is very common, as it is able to give detailed information about the animal's activities (e.g. migration routes, population dynamics etc.) from a distance. Telemetric devices are also used to study physiological aspects, like heart rate and body temperature. However, equipping animals with devices could influence their behavior and ecology. Through literature research the effect of external devices on migratory and aquatic bird species have been determined. It turns out that external devices are causing an increase in drag which strongly affects the flight performance of migrating species and the swimming performance of aquatic species. For migrating species this means that there is an increase in energy expenditure, decrease in migration range and a decrease in return rates for equipped birds. Furthermore, it turned out that bird species migrating longer distances had a stronger decrease in return rates than birds with medium or short migration distance. For aquatic bird species equipped with devices, mostly penguins, the devices were causing an increase in energy expenditure and an increase in diving time. Also a negative correlation with the size of the device (i.e. cross-sectional area) and swimming speed and diving depth was determined for some penguin species. The results strongly point out the importance of being critical as it comes to using telemetric devices. It is suggested that researchers try to minimize the effects of the devices by first studying the effects of the device on the animal (literature of practical research) and stay critical as it comes to interpreting their data.

1. Introduction

Telemetry (from the Greek *tele*, far, and *metros*, measurement) has broadened ecological research in a way that it partly overcomes the shortcomings of our visual capacity (Ropert-Coudert and Wilson, 2005). Whereas previously free-roaming animals were observed from a distance with the many limits this entails, scientists are now able to use telemetric devices to study aspects like migration, activity patterns and even heart rate and body temperature (White *et al*., 2012 and references therein). In particular, avian research has benefited greatly from telemetry, because birds are usually difficult to track over the long distances they migrate. However, for scientific research based on telemetry it is crucial that the devices solely log or transmit data, without influencing the bird and thereby the data themselves (White *et al*., 2012). Nonetheless, negative effects of the devices (including harness) on birds have been documented in the past and although many improvements have been made over the years (e.g. decreases in size and weight) acknowledging and understanding the effect of telemetric devices is essential (Barron *et al*., 2010). Even-more now the use of telemetry in avian research is growing and the demand of studying even smaller birds is high.

The importance of studying the effects of external devices and being critical as it comes to data obtained from research is convincingly demonstrated by Guthery and Lusk (2004). They surveyed 58 reported survival estimates of northern bobwhites (*Colinus virginianus*) and compared these with the empirical expectations of their production. According to the telemetry-derived data, populations of northern bobwhites had alarmingly low survival estimates with an expected extinction of some of the populations in three years. However, Guthery and Lusk (2004) were able to declare 83% of the survival estimates not reasonable. They suggested that the survival estimates were incorrect and the devices were possibly handicapping the bobwhites. Igual *et al.* (2004), on the other hand, stated that the use of loggers is reliable in the case of seabirds at sea. However, both Guthery and Lusk (2004) and Igual *et al*. (2004) do acknowledge that telemetry-derived data should be interpreted carefully and critically. It is clear that telemetric devices have the capacity to (but not necessarily do) influence the model organism, resulting in undesirable data. This report will be limited to bird species, although telemetry is also used in other animal based research.

There are several aspects of telemetric devices that are able to affect the behavior of birds and that are important to consider when using them for scientific purposes. The way devices are being attached to birds, for example, is able to vary between the type of device and the type of bird (e.g. swans are able to carry devices using a neck collar, whereas smaller songbirds are not). Furthermore, devices are able to include an antenna or not and the type of materials used for attachment (e.g. tape, glue etc.) could differ. Also the size and shape of devices is important to consider. The size, more specifically the cross sectional area, of the device could increase drag in both aquatic (e.g. during swimming) and migrating terrestrial bird species (e.g. during flying). By increasing drag, flight and swimming performances could be affected. Another important aspect is the weight of the device relative to the animal's body weight (figure 1). Generally, scientists obey to the "5% rule" which assumes that if the total tag weight (device including harness) is weighing less than 5% of the animal's body weight the effects are negligible. This assumption was made by Brander and Cochran (1969) and not supported by an experimental study. Aldridge and Bringham (1988), however, tested this "5% rule" by varying the mass loads on bats and observed a correlation between mass loads and decreased maneuverability. In contrast, Barron *et al*. (2010) performed an meta-analysis on 84 avian studies and did not find evidence for a general relation between tag weight and bird behavior. Although the effects of added weight are not conclusive, scientists will usually aim at using devices of minimal weight. Nowadays, scientists are even adopting the "3% rule"(Barron *et al*, 2010).

Figure 1. The possible effects of device weight on the behavior and survival of birds (Kenward, 2001)

Through literature research the effects of telemetric devices on birds will be indentified. First the different types of devices and their way of operation will be discussed to be able to understand and interpret the literature used. Furthermore, the influence of devices on several behavioral and physiological aspects of birds will be discussed. Starting with the effects of devices on the flight performance of migrating bird species, followed by the effects on the swimming performance of aquatic bird species and finishing with the effects on physiological aspects of different bird species. In order to get a clear vision of the effect of telemetric devices on birds, swimming and flying bird species will be discussed separately, as they differ greatly in lifestyle. Additionally, other aspects regarding telemetric devices will be discussed, like the effect of different attachment material. The hypothesis underlying this study is that the possible influence of logger devices on birds is unjustly neglected in a large amount of scientific studies. Furthermore, we expect that migrating and swimming of birds is influenced by external devices. The report finishes with some recommendations regarding the use of telemetric devices in the field of ornithology. More knowledge about this subject will strengthen ecological research with telemetric devices and will help limiting the effects of the devices.

2. Telemetric devices

Several strategies have been developed over the years to study the migration patterns, physical condition and the behavior of birds. This has given us more information about their physical and ecological variables, and was the first step in overcoming the difficulties of studying free-living birds. In particular studying migration pattern have been facilitated due to the upcoming of tracking methods. Migration can be studied indirectly, through the use of stable isotopes or genetic markers (box 1), or directly, by attaching tracking devices to the animal. Stable isotopes and genetic markers are both strategies that have important disadvantages and are only able to offer information on a large geographical scale. One of the direct approaches for tracking birds is ringing or banding. This has been proven to be an important way to collect information about migration and wintering grounds for smaller birds. For a long time ornithologists were limited to ringing, because telemetric devices had not been developed yet and the first developed tracking devices were too heavy to be carried by small birds. Unfortunately, the recovery rates of ringed birds is extremely low. For example, Bächler *et al.* (2010) ringed 4101 European Hoopoes (*Upupa epops epops*) all over Europe between 1998 and 2008 and were not able to recover any of the rings at their wintering grounds in Africa. Nowadays, a lot of avian research is based on telemetric devices such as radio transmitters, geo locators, GPS loggers and satellite transmitters.

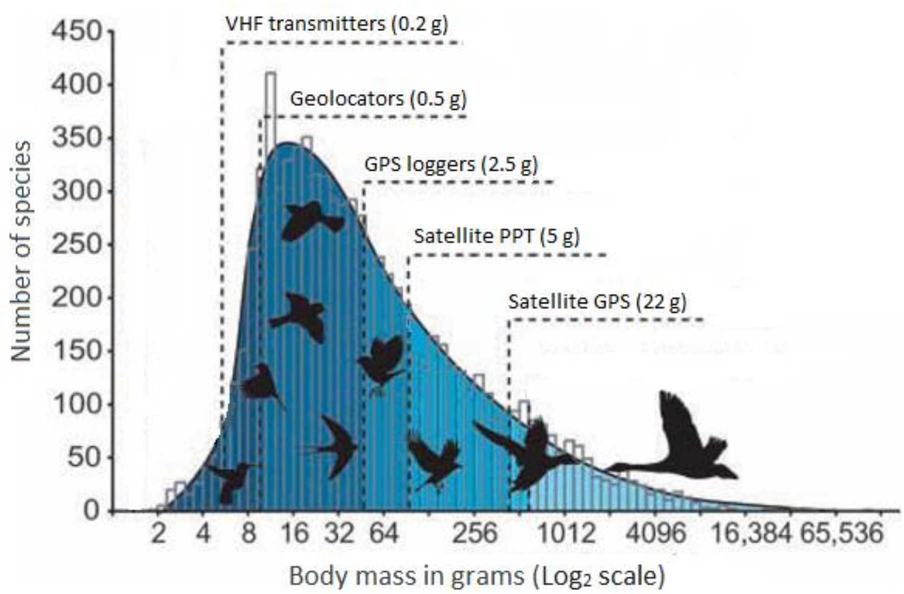


Figure 2. Minimal bird weight (x-axis) for each technology according to 5%-body-weight rule in relation to the number of bird species (y-axis). Weight of the devices might be different when using different type of battery or potting material. Figure adjusted from Bridge *et al*. (2011).

Radio transmitters

Radio transmitters are relatively simple high frequency (VHF) transmitters attached to a bird using an anchor, securing it to the feathers (e.g. by means of glue) or by internally implanting the device (Food and Agriculture Organization (FAO), 2014). Currently, the minimal weight of VHF transmitters is 0.2 g (Naef-Daenzer *et al*., 2005), which means that VHF transmitters can be used for a large group of bird species according to the "5% rule" (figure 2). However, the weight of VHF transmitters might exceed 0.2 g when using a different type of battery (i.e. for a longer duration a heavier battery is needed) or different type of potting material. This applies to all tracking devices. VHF transmitters consist of a battery, an antenna and a transmitter and work through the emission of electromagnetic signals at a particular radio-wave frequency. These signals are subsequently detected using receivers tuned to that specific frequency (FAO, 2014) which have to be in close proximity (within a few km) of the transmitter to be able to detect the signal. This makes tracking birds over long distances practically impossible, unless extreme efforts are being made and the animal is being followed by means of a mobile antenna (Bridge *et al*, 2011). The accuracy of VHF transmitters is quite variable. If tracking is combined by visual sightings the accuracy is rather high (5 m), but when this is not possible, accuracy is usually lower (up to 1 km) (FAO, 2014). Nevertheless, a lot of improvements have taken place over the years. This have made it possible to study even physiological aspects of the birds like heart rate and body temperature (Bridge *et al*, 2011).

Box 1.

Stable Isotopes: Stable isotopes are atoms of a chemical element that have an identical number of protons in the nucleus, but differ in the number of neutrons. Concentrations of these isotopes like deuterium, a stable isotope of hydrogen, vary across the continents. In the case of deuterium, this is the result of precipitation differences, as deuterium reaches the earth through rain or snow. The stable isotopes are taken in and being incorporated in animal tissue as birds forage. By measuring isotope concentrations in animal tissue, the location where the tissue was formed can be determined. This can be used to identify the animal's origin and migration pattern (Robertson, 2004).

Genetic markers: It is possible to study animal dispersal using genetic markers if the genetic variation between populations of the same species is dispersed geographically (i.e. at breeding ground). In that case, birds caught at their overwintering destinations could be traced back to their breeding grounds by using their genetic information. The use of genetic markers is based on comparing a (particular) section of a DNA sequence (i.e. identical within a population) of an individual with that of a genetic marker. A genetic marker is generally a short DNA sequence that contains genetic information of a particular species or a population within a species (Webster *et al.,* 2002; Clegg *et al.,* 2003).

Geo locators

Geo locators, also known as light-level geo locators or global location sensing (GLS) (Catry *et al*., 2010), are used in avian research to record the migration patterns of birds over a long time span (years). Geo locators are generally attached to birds using a leg band (figure 3) or a harness (e.g. backpack) and are one of the lighter tracking devices (Fox and Miet, 2009). The minimal weight of geo locators is 0.5 g (figure 2) which makes them very suitable for studying small birds (<100 g). They are equipped with an internal memory, a clock, batteries and a photoreceptor to record the incoming light. During migration geo locators measure the ambient light level (solar irradiance) and log this data in the internal memory. Afterwards, the time of sunrise and sunset is determined for each day of the elapsed period. This is used to estimate the location of the bird on each particular day. In order to determine the latitude of the location the length of the day is used. For example, in June the further north the bird would fly the longer the days are and in December the other way around.

Figure 3. Notern wheatear (*Oenanthe oenanthe*) tagged with a geo locator using a leg band (Arlt *et al*., 2013).

For the days around March 21 and September 21 it is not possible to calculate latitude because day lengths are the same all over the globe, known as equinoxes. It is, fortunately, possible to use the length of the twilight to estimate the location. The longitude can be determined by the time of midway between sunrise and sunset (local noon) or between sunset and sunrise (local midnight) (Afanasyev, 2003). The reliability of geo locators is not always optimal, as the position estimates are influenced by shading (e.g. trees, covering by feathers) and movements of the animal (Bridge *et al*., 2013; Bächler *et al*., 2010). This makes it impossible to determine the bird's exact location (latitude error ≥200km) and makes it more appropriate for long distance migrants. Additionally, in order to retrieve the data the geo loggers have to be recovered. Besides geo locators being lost by birds, recovery rates of birds carrying a geo locators are often very low. Nevertheless, geo locators have provided the ornithology field with more knowledge about timing and routes of birds during migration (Bridge *et al*., 2013).

GPS logger

Another telemetric device is the GPS logger, that works, like the name reveals, with the Global Positioning System (GPS) and 25 US satellites around the globe. GPS loggers (figure 4) have a minimal weight of 2.5 g and are attached by securing it to the feathers (e.g. by using tape) or with a harness. GPS loggers are equipped with an (fractal or ceramic) antenna, a power supply of solar cells and/or a battery, a GPS receiver and a logger (Bouten *et al*., 2013). The GPS receiver picks up signals emitted from satellites and calculates the geographical location of the bird at that moment. The logger records and stores this data at a pre-determined time interval. GPS loggers have an unlimited range and are

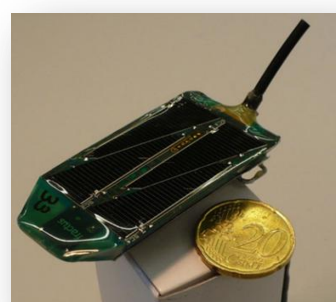


Figure 4. A GPS logger with the antenna. Coin represents the size of the logger (Bouten *et al*., 2013).

very precise (accuracy of ±5 m) (Bridge *et al*., 2011). Another benefit from this type of telemetric devices is that recapture of the animal is not always necessary, because a bi-directional remote data transmission can be implemented in the device. This means that data can be downloaded from the device and new programs can be uploaded to the device without having to recapture the device from the bird (Bouten *et al*., 2013).

A relatively new innovation is the GPS GSM logger. This type of logger works analogous to the GPS logger except instead of solely logging the data, it is also able to transmit the data using the GSM (Global System for Mobile Communications) network. The location data is being stored internally and only when the GSM reception is adequate the information is transmitted to the GSM network. This enables the device to make more efficient use of the battery, as it does not have to constantly transmit data. The combined GPS GSM loggers is a relatively new and improvements regarding size and weight are still needed (Bridge *et al*., 2011).

Satellite transmitter

Satellite telemetry as a way to study animal dispersal has already been used for a few decades. It started with large vertebrates, but due to many technical improvements and advances in minimization (reduce size/weight and use of solar panels) it is currently possible to study birds (Soutullo *et al*, 2010 and references therein). There are two types of satellite transmitters: the Platform Terminal Transmitter (PTT), with a minimal weight of 5 g, and the Global Positioning System (GPS) transmitter, with a minimal weight of 22 g (figure 2). Generally the devices are attached to the animal using backpack style, collar or by implanting the device. In contrary to VHF radio transmitters, PPT and GPS transmitters are much more advanced (e.g. option for solar panels instead of batteries) and use orbiting satellites to automatically transmit and receive signals. The PTT transmits radio signals of a particular wavelength that are being picked up by orbiting signals as they pass overhead. The position of the PPT, and the bird bearing it, is estimated using the Doppler effect. This states that due to the difference in speed of the bird with the PPT (the transmitter) and the orbiting satellite (the receiver) the frequency of the transmitted wavelength signal is changed. By using this change in frequency the ground based part of the satellite system is able to determine the location of the bird (Fancy *et al*, 1988). The accuracy of both the PPT and GPS transmitter are relatively good, within 100-200 m and 10-20 m respectively. The latter being more accurate, but also larger and more expensive. In order to collect the data the bird do not have to be recaptured, as the data is transmitted to a receiving station.

3. The effect of telemetric devices on flight performance

Every autumn millions of birds fly long distances to warmer southern regions with higher food availability to avoid the severe winter of the North. The specific routes they migrate have long been a mystery, but due to the upcoming of tracking devices, unraveling their migration patterns have become a possibility. However, the addition of a device could strongly influence the flight behavior of the animal. For example, the size and shape of these devices could increase the aerodynamic drag which is a great concern especially for migrating birds.

Aerodynamic drag

Although tracking devices are widely used in studying migration, little attention has been devoted to the effect of the added drag of these devices on migrating birds. Only a limited number of studies are known to have addressed this topic according to Bowlin *et al*. (2010) and personal observation. In 1987 Obrecht *et al*. measured the aerodynamic drag of radio transmitters using a wind tunnel and preserved bodies of different bird species and used this to estimate the effect of drag on a bird's flight performance. In doing so, they used four different shaped dummy transmitters (figure 5), in which shape A consisted of a relatively simple shaped rectangular box and the three other shapes (B, C and D) had, in addition of the same basic box, streamlined fairings. Furthermore, to test the influence of added load, the dummy transmitters were differing in weight (size 1; 30 g, size 2; 80 g and size 3; 160 g). It turned out that the shape causing the highest increase in drag was shape A, the only unfaired dummy transmitter. The addition of fairings on the front end and a fairing behind (going from shape A to C) caused a reduction in drag by one-third. This was seen for transmitters of size 2 and 3. Measuring the drag for transmitters of size 1 was unsuccessful as it was too small for the equipment used to measure.

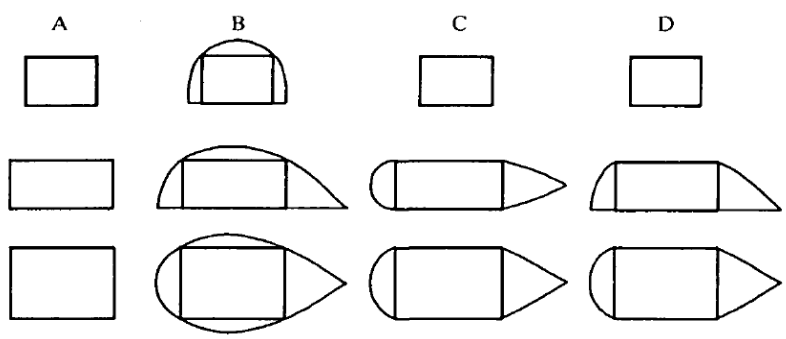


Figure 5. The four shapes of dummy transmitters in front view (upper), side view (middle) and top view (lower). The frontal end of the transmitter faces left in the side and top views (Obrecht *et al*., 1987).

Drag has an effect on the flying performance of birds, for example on the migrants range (i.e. distance a bird can fly until the stored fat is used up). As was shown by estimating the migrants range of a snow goose (*Chen caerulescens*) carrying no transmitter (control), a dragless transmitter, a transmitter of shape A or a transmitter of shape C of size 2 or 3 (table 1). The addition of solely weight (the dragless transmitter) was only causing a small decrease in migrants range, 47 km and 93 km for size 2 and 3 respectively, compared to control. A stronger decrease of migrants range was seen with transmitter shape A, 182 km for size 2 and by 299 km for size 3 compared to control. However, when Obrecht *et al*. (1987) compared the migrants range of shape A with shape C, strongly differing in the amount of drag, there was an increase in range of 41 km and 61 km, for size 2 and 3 respectively.

Table 1. Calculated ranges for snow Goose with different transmitters.

Transmitter	Mass (g)	Range (km)	Change (km)
None		1845	
2 (dragless)	80	1798	47
2A	80	1663	182
2C	80	1704	141
3 (dragless)	160	1752	93
3A	160	1546	299
3C	160	1607	238

Obrecht *et al*. (1987) concluded from these results that the optimal shape for a transmitter used on birds should have rounded fairing in the front and pointed end fairings (as seen with shape C). This shape will have the lowest amount of drag and therefore a smaller decrease of the migrants range. It appears that drag is having an high impact on migration of birds, more than the addition of weight. However, the study of Obrecht *et al*. (1987) only looked at the effect of the transmitters on the migrants range. It might be possible that the effect of weight is only observed when the bird is feeding its nestlings, foraging or during other activities besides migration.

It turns out other studies are observing an effect of aerodynamic drag on flying performance as well. For instance, Stutchbury *et al*. (2009) studied the migration routes of a population purple martins (*Progne subis*) and a population wood thrushes (*Hylocichla mustelina*) using geo locators. The population of purple martins was located in North Pennsylvania (USA) and had their wintering grounds in South Africa. In the beginning of June (2007) 20 purple martins (11 males and 9 females) were captured at their breeding grounds and fitted with a geo locator (1.5 g, attached using leg-loop harness). Additionally a subset of birds was only banded (number not published) with a leg band. A year later, in May (2008), the birds, back from their wintering grounds, were recaptured and the geo locators were removed. Of the initial 20 purple martins carrying a geo locators, they were only able to recapture 10% (2/20). And of the birds only carrying leg bands 54% was recaptured. This could indicate that the devices are lowering the changes of the equipped purple martins to return safely from their winter migration, possibly through increasing drag. However, the data from the population of wood thrushes is not showing a similar result. The population of wood thrushes, also breeding in North Pennsylvania (USA) had their wintering grounds in Central America. In August (2007) 14 wood thrushes (7 males, 7 females) were captured and fitted with a geo locator. Additionally, 67 birds (32 males, 35 females) were only banded with a leg band. The following year (2008), 50% (7/14) birds fitted with a geo locators were resigned and 56% (18/32) males and 11% (4/35) female birds carrying a leg band were recaptured. The recapture rate of males was higher, because females have less territory site fidelity. According to Bowlin *et al*. (2010) the percentage of recaptured wood thrushes with geo locator was normal (i.e. compared to return birds with leg bands), but this was not the case for purple martins. They suggested that there was a difference in the effect of drag of the device on two bird species due to the differences in migration distance (figure 6). Purple martins are long distance migrants and therefore possibly more affected by an increase in drag than wood thrushes, a median distance migrant. Furthermore, purple martins are aerial insectivores, which means that they feed primarily on flying insects. The weight of the device could also have different effect on purple martins than wood thrushes, as they might differ in body mass. However the weight of the purple martins studied by Stutchbury *et al*. (2009) was between 43-54 g (n=20) and for wood thrushes between 47-55 g (n= 14). Because these numbers do not differ greatly from each other, it is unlikely that the weight of the device would have a different effect on the migration of purple martins than on wood thrushes.

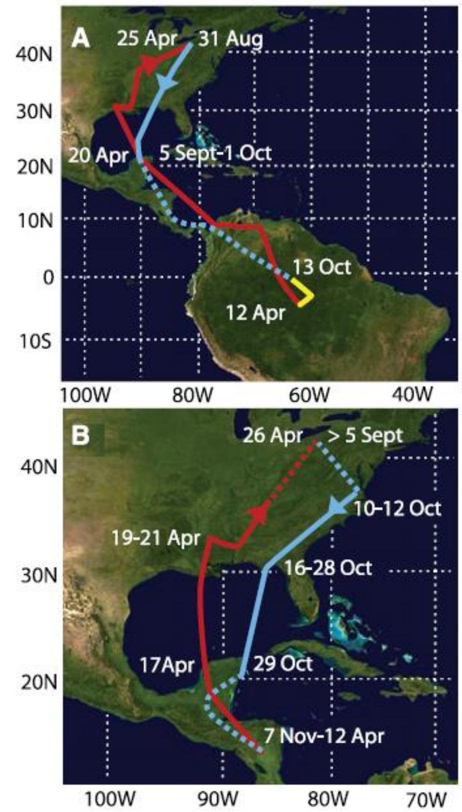


Figure 6. Purple martins (A) and wood thrushes (B) that bred in Pennsylvanian, USA. Blue, fall migration; yellow, winter movements; red, spring migration. Dotted lines where latitude could not be calculated (Stutchbury *et al*., 2009).

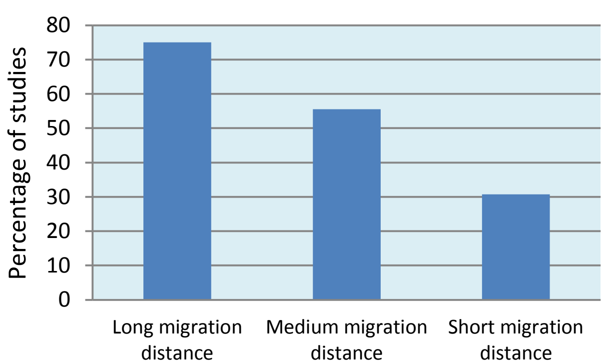
Bowlin *et al.* (2010) confirmed the effect of drag seen in the study of Stutchbury *et al*. (2009) by testing three different geo locators on preserved (wingless) common swift (*Apus apus*) bodies, which has morphological similarities with the purple martin, using a wind tunnel. The dimensions of the three different geo locators are: 1 (1.2 g and 56.76 mm^2), 2 (1.0 g and 34 mm^2) and 3 (0.5 g and 31.16 mm^2) and were attached using backpacks harness. Two out of the three different geo locators showed a significant increase in drag. Interestingly, the one causing no significant increase in drag was the one of medium weight, but with a more flat design and the smallest frontal area (mm^2). In this design the battery was placed in front instead of on top of the electronics. Even-though the effect of the device's cross sectional area seems to exceed the effect of weight Bowlin *et al*. (2010) concluded that added weight and drag have a similar effect on the fight range.

Another study, convincingly demonstrating the effects of drag on flying performance is a study of Gill *et al*. (2009). They studied the migration of bar-tailed godwits (*Limosa lapponica baueri*) using internal and external transmitters. In June (2006) 7 female godwits were captured and received an internal PTTs weighing 26 g. At the same time, 2 male godwits were fitted with an external PTT weighing 10.5 g. Since male godwits weigh less than female godwits, they were only able to carry the lighter external PTT. Subsequently the migration routes were determined for the two groups of godwits. It turned out that the female godwits, with the heavier implanted devices, covered a distance of 81171-11689 km, whereas the male godwits, with the lighter external transmitter, covered a distance of 7008-7390. Gill *et* *al*. (2009) state that the two male godwits were affected by the drag of the transmitter and that this had effected their flight performances and thus the distance they were able to cover in a non-stop flight.

Return-rate

Return rate is the proportion of animals in a study (of the total number of animals in the study) that were either recaptured or re-sighted after migration and represent the survival estimates of the animal. Numerous avian studies using tracking devices mention the return rates of the birds with tracking devices and the birds without (i.e. controls, usually only ringed). If tracking devices would affect survival during migration the return rates would be lower for the bird carrying an external tracking device. Bridge *et al*. (2013) reviewed 38 published and unpublished studies involving different species of migrating birds and did not find a general evidence for geo locators negatively affecting survival. Of the 38 studies, only 24 mention both recovery rate for geo logged and ringed (control) individuals. Of these, 9 (38%) studies report a decreased recovery rate of birds carrying a geo locator, of which 5 (21%) have a decrease of more than 10%. However, this review might give a biased view as it incorporates studies with low replica's and with methodological differences (i.e. mounting material). In table A1 (appendix) the data derived from Bridge *et al*. (2013), collectively encompassing 40 different cases have been complemented with an estimation of migration distance. Of the 40 cases, ten studied bird species that were defined as long distance migrants, twelve as medium distance migrants and eighteen as short distance migrants. For each migration strategy we calculated the proportion of species for which 'return bands only' exceeded 'return geo loggers' (figure 7a; only cases were both returns bands and returns geo loggers have been mentioned are incorporated).

a)



b)

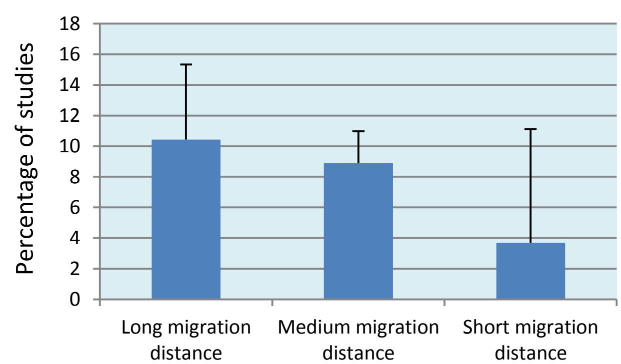


Figure 7. a) The percentages of cases were the percentage of return bands only exceeded the percentage of returns geo loggers. Long distance migrants (75%: n=8), medium migration distance (55,56%; n=9) and short migration distance (30.8%; n=13). B) The average difference in percentage between return bands only and return geo loggers (% return bands - % returns geo loggers) between the different groups.

significant (ANOVA, p>0,05), is seen when comparing the average differences between 'return bands only' and 'return geo loggers' (figure 7b). Generally it looks like long distance migrants experience more negative effects of the addition of a geo locator than medium and short distance migrants. This further supports the findings of Stutchbury *et al.* (2009) who found significantly more negative effects of the geo logger when attached to a long distance migrant compared to a medium-distance migrant. This is due to the fact that long distance migrants have to fly a longer distance during migration, the effect of drag of the device, even-though possibly minimal, is more when the bird has to spend more time in the air.

4. The effect of telemetric devices on swimming performance

The influence of telemetric devices on flying bird species is partly revealed in their ability to fly long distances (e.g. migrants range) and in their survival. However, whereas flying birds experience the effects of an increase in drag by carrying devices through air, aquatic birds face a much larger challenge by having to carry the devices through water, a far more dense and viscose medium than air. Since swimming birds have to push the external devices through water, more energy is spent (in Vandenabeele *et al*, 2011). The effects of telemetric devices on aquatic birds have been studied frequently, as they are able to affect behavior and survival to a great extent. The addition of an external device is adding both weight and hydrodynamic drag which could affect the bird's swimming performance. Externally attached devices are disrupting the flow of water over the highly streamlined bodies of aquatic birds and in doing so strongly affect diving and swimming performances (Ropert-Coudert *et al*., 2007). This in turn, has a great influence on foraging behavior and survival, as it affects the ability to catch prey.

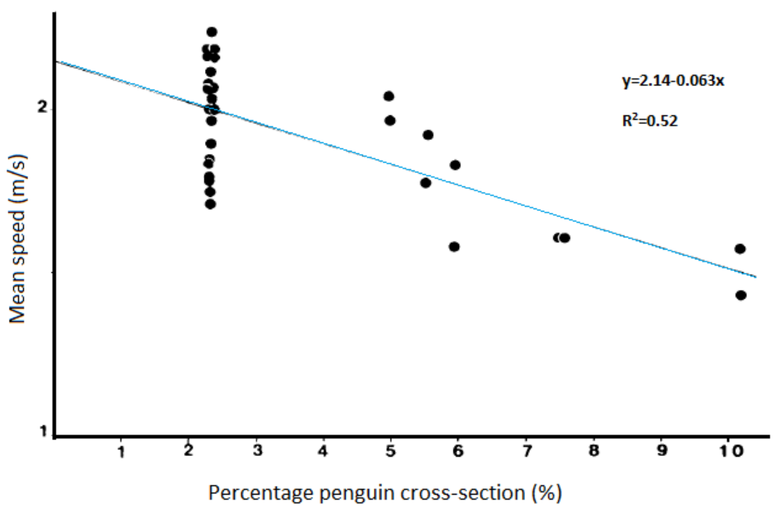


Figure 8. Correlation between mean speed (y-axis) during foraging trips and percentage cross-sectional area (x-axis) of an attached device relative to the frontal cross-sectional area of an African penguin (Wilson *et al*., 1986).

Hydrodynamic-drag

The drag added by carrying external devices through water is affecting swimming birds, of which penguins are the most predominant as they spend a lot of time foraging in great depths. Because literature on the effect of telemetry devices on swimming performances almost exclusively focuses on penguins, the effects of hydrodynamic drag will be solely discussed regarding these bird species. In studying the hydrodynamic drag, scientists do not (solely) focus on the weight of the device, but especially on the cross-sectional area (in cm^2) of the device relative to the frontal cross-sectional area of the bird. This is shown by Wilson *et al*. (1986), who observed a negatively correlation between the cross-sectional area of an externally attached device and the mean swimming speed (figure 8) of the African penguin (*Speniscus demersus*). Additionally, Wilson (1989) negatively correlated the cross-sectional area of the device with the maximum diving depth during foraging trips of Adélie penguins (*Pygoscelis adeliae*) and Gentoo penguins (*Pygoscelis papua*) (cited by Culik *et al*., 1993). In addition Culik et al. (1993) observed a reduction of 8.3% in swimming speed compared to unequipped controls for adelie penguins. Furthermore, the energy expense of device equipped Adélie penguins was increased with 42% (Culik and Wilson, 1991), possibly because diving activities were requiring more energy (Wilson and Culik, 1992). In a study of Ropert-Couder *et al*. (2007) the effects of two different sized devices on little penguins (*Euduptula minor*) were compared. The larger device was covering 4.9% of the birds frontal area and the smaller one 3.4%. Penguins equipped with the smaller devices made significantly longer (16%), but fewer dives (37%). Additionally they were spending less time (16%) underwater in comparison to the penguins carrying the larger device. This could mean that they were more efficient in catching prey than penguins carrying the larger devices, because the smaller devices were causing less drag. This is supported by Ludynia *et al*. (2012), who found that Southern rockhopper penguins (*Eudyptes chrysocome*) carrying larger devices were less dive efficient as they were making more dives per foraging trip implying that they had to try more times to catch prey, and were therefore spending more time underwater.

Another approach to study the effect of drag created by external devices is using internally implanted devices as a (secondary) control group. In doing so, the effect of solely the drag and not the weight of the device can be tested. Ropert-Coudert *et al*. (2000a) used this method to investigate if the attachment of external devices is affecting the diving performance (e.g. dive depth and frequency) and thereby foraging behavior of King penguins (*Aptenodytes patagonicus*, figure 9). They found that the penguins with externally attached devices had a lower frequency of diving to great depths in comparison to birds with implanted devices. Additionally, Culik and Wilson (1991) found that Adélie penguins with implanted devices were swimming at a lower speed than the controls (no devices), and the penguins with external attachments had a bimodal speed distribution (i.e. continuous distribution with two maxima). Furthermore, the power input (W kg^{-1}) and costs of device transport (J $kg^{-1}m^{-1}$), showed large differences. However, the bimodal speed distribution of device equipped penguins could be addressed to the observation that penguins equipped with devices showed more unrest behavior (unquantifiable activities), possibly because they wanted to get rid of devices. In addition, this group had a higher pecking frequency. Furthermore, the power input and costs of transport for penguins with implanted devices was 20% and 23% less than controls, respectively. The power input and costs of transport of penguins with external devices, however, was 42% and 25% more than controls, respectively. Generally, the use of internal devices would seem better than external ones,

Figure 9: Swimming King penguins (Worldpress, 2014).

because drag would be minimized and less energy would be consumed. However, removing external devices is easier than for internally placed devices and the consequences for the animals after the experiment are minimal (Culik and Wilson, 1991). The weight of the device does not seem to be affecting behavior of most of the swimming bird species such as penguins, which are able to ingest meals weighing up to 26% of their body mass, and the weight of the devices usually does not exceed 1% of the body mass (Wilson *et al*., 1986).

5. Additional effects

Aside from the impact of external devices on the swimming and migrating performances of the bird, the devices can also have other impacts on birds, like reduced breeding success and the deteriorated physical state of the animal (Robbert-Coudert *et al*., 2007). For example, unrest behavior, like pecking at the device, has been reported by Wilson and Wilson (1989) for both African (Spheniscus demersus) and Adélie penguins. Because this behavior was merely seen while the penguins were at sea, it directly increased the time away from the nest. The color of the device seemed to be of large influence as well, as adjusting the color of the device to the color of the plumage of the animal minimized their pecking behavior. Handling of the animal and the attachment of the devices, in the case of southern rockhopper penguins, had minimal impact (Ludynia *et al*., 2012).

The effects of external devices on the physical condition of birds is shown by Eilliott *et al*. (2012). They measured the corticosterone levels of common murres (*Uria aalge*) and concluded that the levels were twice as high for equipped birds as for controls. Additionally the body masses were lower for equipped murres. There were significant differences between colonies, though. According to Vandenabeele *et al*. (2011) birds with higher wing loadings (i.e. small wing area relative to body weight), like murres, have a higher chance to be negatively affected by external tracking devices in comparison to bird with low wing loadings like shearwaters. This statement is supported by studies of Paredes *et al*. (2003) and Philips *et al*. (2003). Paredes *et al*. (2003) studied thick-billed murres (*Uria lomvia*), and saw that female device equipped murres had a lower body mass, offspring attendance and a lower number of foraging trips than unequipped birds. Furthermore, male thick-billed murres had an increased trip duration, so needed to spend more time foraging due to device. The couples did however compensate for their reduced partner effort. For black-browed (*Thalassarche melanophris*) and gray-headed albatross (*T. chrysostoma*) on the other hand, the study of Philips *et al*. (2003), no significant effects on foraging trip duration, breeding success and return rates have been documented. This can possibly be explained, according to Vandenabeele *et al*. (2010), by the fact that these bird species have lower wing loadings.

6. Effect of different device attachment technique

Until now the effects of solely the telemetric devices on birds have been discussed, without considering the effects of the different attachment techniques. However, there are various ways of attaching devices to birds, like backpack harness, neck collar and leg band. Using a different attachment technique might influence the behavior of the bird. For example, Bowlin *et al*. (2010) measured a higher drag when using a wing harness, attached on the back between the wings, than when using a leg-loop harness, attached on the rump (figure 10). Also the reduction in flight range was more affected by wing harness, than by increasing the weight of the device. Furthermore, Pennycuick *et al*. (2011) found that when devices included an antenna there was an increase in drag coefficient in comparison to devices without antenna's.

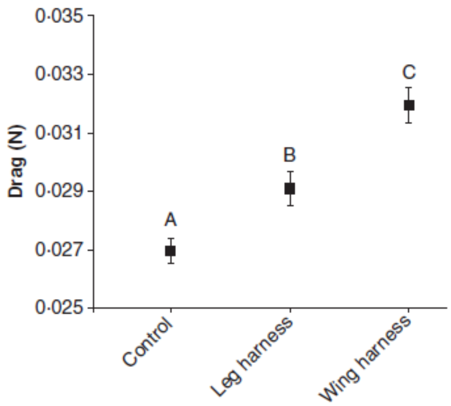


Figure 10. Drag due to geo locators in two different locations. Letters indicate statistically separate groups based on Bonferroni post hoc tests (Bowlin *et al*., 2010).

Table 2. Assessments of different radio tag attachment techniques (XXX = greatest disadvantage). Figure adjusted from Kenward, 2001.

Technique	Handeling time	Skill require-ment	Rate of loss	Risk of effect
Implant	xxx	xxx	x	xx[1]
Body-harness	xx	xxx	x	xxx[2]
Glue (feather)	x	xx	xxx	xx[1]
Bird necklace	x	x	x	xx[1]
Bird patagium	x	xx	xx	xx[1]
Bird beak	x	xx	xx	xx[0]
Bird leg	x	x	xx	x[1]
Bird tail	xx	xx	xx	x[1]

[0]Ratings with no comparisons published.
[1]Ratings based on less than 10 published comparisons.
[2]Ratings based on more than 10 published comparisons.

When comparing different attaching techniques (table 2), there seems to be a difference in the effects. For example, Kenward (2001) suggests that the use of device implantation or body-harness techniques should be avoided, unless devices are needed to record for a long time span. In that case implementation or body-harnesses are most fit, because these have a lower loss rate. When studying birds for just a few weeks, using glue-mounts (i.e. tail or leg mounts) is more appropriate, depending on the type of device.

7. Recommendations

Through literature research it became clear that telemetric devices are able to affect bird behavior. It is recommended that researchers focus on minimizing the cross sectional area of the devices and make a more streamlined design (e.g. addition of fairings in the front and back of the device) in order to minimize the drag which is found to have a great impact on migrating and aquatic bird species. Furthermore the way of attachment could also have effects on birds. Researchers are recommended to study the effects of the device on the animal (literature of practical research), before using them, and stay critical as it comes to interpreting their data.

References

Afanasyev, V. (2003). A miniature daylight leven and activity data recorder for tracking animals over long periods. Mem. Natl Inst. Polar Res., Spec. Issue 58, pp: 227-233

Aldridge, H. and Bringham, R.M. (1988). Load carrying and maneuverability in an insectivorous bat: a test of the 5% " rule" of radio telemetry. Journal of mammalogy 69, pp: 379 – 382 uit Barron et al. (2010

Arlt, D., Low, M. and Pärt, T. (2013). Effect of geolocators on migration and subsequent breeding performances of a long0distance passerine migrant.

Bächler, E., Hahn, S., Schaub, M., Arlettaz, R., Jenni, L., Fox, J.W., Afanasyv, V. and Liechti, F. (2010). Year-round tracking of small trans-Saharan migrants using light-level geolocators, Open access

Barron, D.G., brawn, J.D. and Weatherhead, P.J. (2010). Meta-analysis of transmitter effects on avian behavior and ecology, Methods in Ecology and Evolution 1, pp: 180 – 187

Bouten, W., Baaij, E.W., Shamoun-Baranes, J. and Camphuysen, K.C.J. (2013). A flexible GPS tracking system for studying bird behaviour at multiple scales, Journal of onrinthology Volume 154, Issue 2, pp 571-580,

Bowlin, M.S., Henningsson, P., Muijres, F.T., Vleugels, R.H.E., Liechti, F. and Hedenström, A. (2010). The effects of geolocator drag and weight on the flight ranges of small migrants, Methods in ecology and evolution 1, pp:389-402

Brander, R.B. and Cochran, W.W. (1969). Radio location telemetry. Wildlife management techniques (ed. R.H. Giles Jr), pp: 95-103 uit Barron et al. (2010)

Bridge, E.S., Kelly, J.F., Contina, A., Gabrielson, R.M., MacCurdy, R.B. and Winkler, D.W. (2013). Advances in tracking small migratory birds: a technical review of light-level geolocation, J. field ornithology 84, pp: 121-137

Bridge, E.S., Thorup, K., Bowlin, M.S., Chilson, P.B., Diehl, R.H., Fléron, R.W., Hartl, P., Kays, R., Kelly, J.F., Robinson, W.D. and Wikelski, M. (2011). Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds, BioScience 61(9), pp: 689-698

Catry, I., Dias, M.P., Catry, T., Afasyev, V., Fox, J., Franco, A.M.A. and Sutherland, J.W. (2010). Individual variation in migratory movements and winter behavior of Iberian Lesser Kestrels Falco naumanni revealed by geolocators. Ibis, 153, pp: 154 -164

Clegg SM, Kelly JF, Kimura M, Smith TB. (2003). Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a neotropical migrant, Wilson's warbler (Wilsonia pusilla), Mol Ecol. 12, pp:819-30

Culik, B. and Wilson, R.P. (1991). Swimming energetic and performance of instumented Adelie penguins (pygoscelis adeliae). J.exp. Biol. 158, pp: 355-368

Eilliott, K.H., McFarlane-Tranquilla, L., Burke, C.M., Hedd, A., Montevecchi, W.A. and Anderson, W.G. (2012). Year-long deployments of small geolocators increase corticosterone levels in murres, Mar Ecol Prog Ser, 466, pp: 1-7

Fancy, S. G., L F. Pank, D. C. Douglas, C. H. Curby, G. W. Garner, S. C. Amstrup, and W. L. Regelin. (1988). Satellite telemetry: a new tool for wildlife research and management. U.S. Fish and Wildlife Service Resource Publication 172, Washington, D.C., USA

Food and Agriculture Organisation (FAO), Radio telemetry and bird movement, retrieved on 10 January, 2014 from: http://www.fao.org/

Fox, J. and Miet, M. (2009). Geolocator manual V7. Retrieved from: http://www.arctictern.info/carsten/pdf/Geolocator_manual_v7.pdf

Gill, R.E., Tibbitts., Douglas, D.C., Handel, C.M., Mulcahy, D.M., Goytschalck, J.C., Warnock, N., McCaffery, B.J. Battley, P.F. and Piersma, T. (2009). Extreme endurance flights by landbirds crossing Pacific Ocean: ecological corridor rather than barrier?, Proceedings of the royal society series 276, pp: 447-458

Guthery, F.S. and Lusk, J.J. (2004). Radiotelemetry studies: are we radio-handicapping northern bobwhites?, wildlife society bulletin 32 (1), pp: 194 - 201

Igual, J.M., Forero, M.G., Travecchia, G., González-Solis, J., Martínes-Abraín, A., Hobson, K.A., Ruiz, X. and Oro, D. (2004). Short-term effects of data-loggers on Cory's shearwater (Calonectris diomedea), Marine Biology 146, pp: 619 – 624

Kenward, (2001). A Manual for Wildlife Radio Tagging, ISBN: 9780124042421

Ludynia, K., Dehnhard, N., Poisbleau, M., Demongin, L., Masello, J.F. and Quillfeldt, P. (2012). Evaluating the impact of handeling and logger attachment on foraging parameters and physiology in southern rockhopper penguins, Open access

Naef-Daenzer, B., Früh, D., Stalder, M., Wetli, P. and Weise, E. (2005). Miniaturization (0.2 g) and evaluation of attachment techniques of telemetry transmitters, Journal of experimental biology 208, pp: 4063-4068

Obrecht, H.H., Pennycuick, C.J. and Fuller, M.R. Wind tunnel experiments to asses the effect of back-mounted radio transmitters on bird body drag, J. exp. Biol. 135, pp: 265-273

Paredes, R., Jones, I.L. and Boness, D.J. (2003) et al., 2003). Reduced parental care, compensatory behavior and resproductive costs of thick-billed murred equipped with data loggers, Animal behavior 69, pp: 197-208

Philips, R.A., Xavier, J.C. and Croxall, J.P. (2003). Effect of satellite transmitters on albatrosses and petrels, the Auk 120, pp: 1082-1090

Robert-coudert,Y., Knott, N., Chiaradia, A. and kato, A. (2007). How do different data logger sizes and attachment positions affect the diving behavior of little penguins?, Deep-Sea research II 54, pp:415-423

Robertson, B.A., Forging new links in bird migration, retrieved on 10 January, 2014 from: https://www.aba.org/birding/v36n2p142.pdf

Ropert-Coudert, Y. and Wilson, R.P. (2005). Trends and perspectives in animal attached remote sensing, Front Ecol and environ 3, pp: 437 - 444

Ropert-Coudert, Y., Bost, C.-A., Bevan, R.M., Handrich, Y., Le Maho, Y., Woakes, A.J. and Butler, P.J. (2000a). Impact of externally-attached logger on diving behavior of the king penguin (Aptenodytes). Physiological and biochemical zoology 74, pp: 438-444

Soutullo, A., Cadahia, L., Urios, V., Ferrer, M. and Negro., J.J. (2010). Accuracy of Lightweight Satellite Telemetry: a Case Study in the Iberian Peninsula, The Journal of Wildlife Management, Volume 71, Issue 3,pp: 1010-1015

Stutchbury, B.J.M., Tarof, S.A.., Done. T., Gow, E., Kramer, P.M., Tautin, J., Fox, J.W. and Afanasyev, V. (2009). Tracking long-distance songbird migration using geolocators, science 323, pp: 896-896

Vandenabeele, S.P., Wilson, R.P. and Grogan, A. (2011). Tags on seabirds: How seriously are instrument-induced behaviors considered?, Universities federation for animal welfare 20, pp: 559:571

Webster, M.S., Marra, P.P., Haig, S.M., Bensch. S., **Holmes**, R.T. (2002). Links between worlds: unraveling migratory connectivity, Trends in ecology and evolution 17, pp: 76end

White, C.R., Cassey, P., Schimpf, N.G., Hasley, L.G., Green, J.A. and Portugal, S.J. (2012). Implantation reduces the negative effects of bio-logging devices on birds, The journal of experimental biology 216, pp: 537 - 542

Wilson, R.P. (1989). Diving depths of Gentoo pygoscelis papua and adelie pygoscelis adelia penguins at esperanza Bay, Antarctic Peninsula. Cormorant 17, pp:1-8

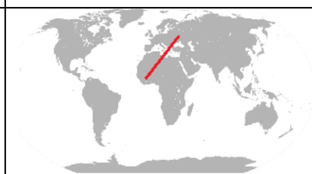
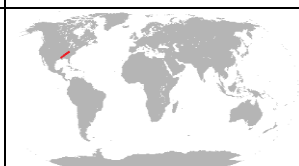
Wilson, R.P. and Culik, B. (1992). Packeges on penguins and device induced data. In priede, I.G., Swift, S. (eds.) Wildlife telemetry, Ellis Hornwood, pp: 573-580

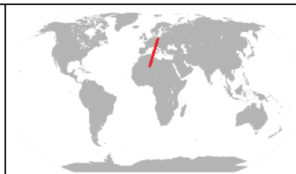
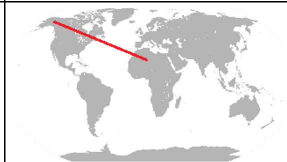
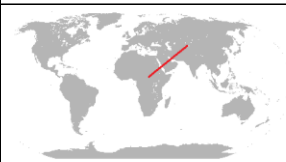
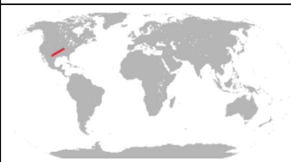
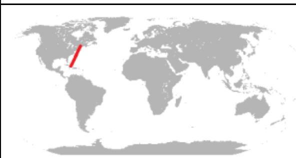
Wilson, R.P., Grant, W.S. and Duffy, D.C. (1986). Recording devices on free-ranging marine animals: does measurement affect foraging performance?, Ecology 67, pp: 1092-1093

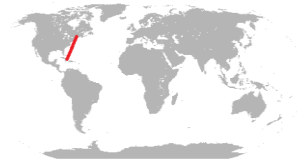
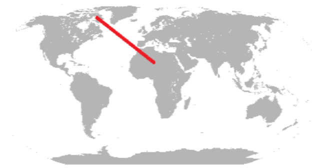
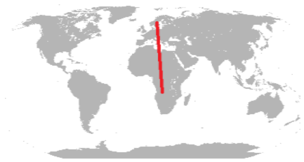
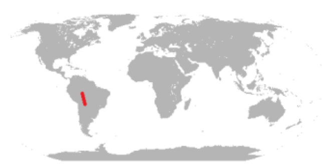
Worlpress, 2014, retrieved from: http://whyevolutionistrue.wordpress.com/2011/10/19/time-to-put-andrew-brown-to-pasture/under-threat-king-penguins-off-the-coast-of-macquarie-island/

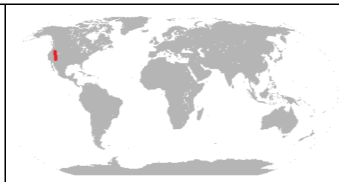
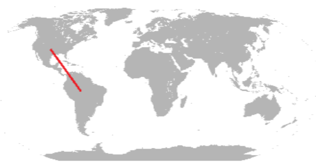
Appendix

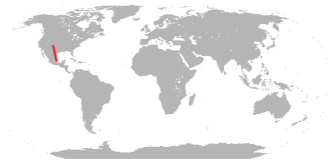
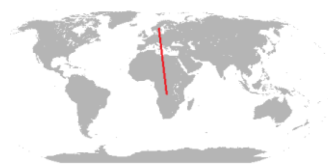
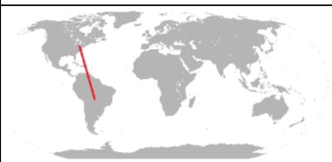
Table A1: Species, return rates, tag weight (from which % of body weight has been calculated) and location data derived from Bridge *et al* (2013). Migration distance estimated using birdslife.org.

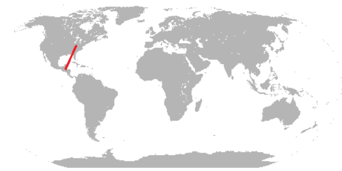
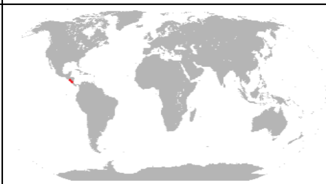
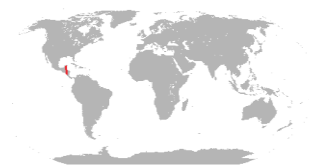
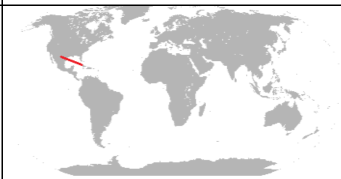
	% of body weight	Return, geo locators	Returns, bands only	Location	Migration distance (map)	Distance:	source
Pied Flycatcher (*Ficedula hypoleuca*)	5	17/59 (29%)	37/135 (27%)	Netherlands		Medium	C. Both and J. Ouwehand (unpubl.)
Aquatic Warbler (*Acrocephalus paludicola)*	5 – 5,583	6/30 (20%)	6/16 (38%)	Ukraine		Long	Salewski *et al*., 2013
Painted Bunting (*Passerina Ciris)*	4 – 5,33	45/200 (23%)	15/97 (15%)	Oklahoma		Short	Contina *et al*., in press
Tree Swallow (*Tachycineta Bicolor)*	3,5 - 4	19/71 (27%)	-	New York, Wisconsin		Short	A. Laughlin, L. Whittingham, P. Dunn, and C. Taylor (unpubl.)
Red-eyed Vireo (*Vireo olivaceus*)	3,5	10/26 (39%)	5/11 (45%)	Pennsylvania		Long	Callo *et al*., (in press)

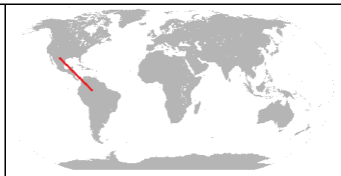
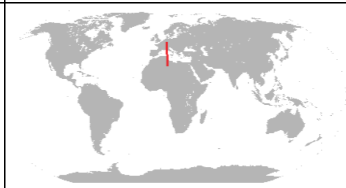
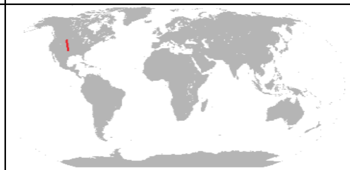
Northern Wheatear (*Oenanthe Oenanthe)*	6,09	9/20 (45%)	58/107 (54%)	Germany		Medium	Schmaljohann *et al.*, 2012
Northern Wheatear	5,6	5/30 (16%)	N/A	Alaska		Long	Bairlein *et al.*, 2012
Northern Wheatear	2,69 – 3,07	16/60 (20%)	N/A	Mongolia		Medium	N. Batbayar and E. Bridge (unpubl.)
Thrush Nightingale (*Luscinia luscinia*)	3,46	10/44 (23%)	37/167 (22%)[a]	Scandinavia		Medium	Sorjonen 1987, Stach *et al.*, 2012, Tøttrup *et al.*, 2012a
Lark Sparrow (*Chondestes grammacus*)	2,69 – 3,07	9/21 (43%)	50/81 (62%)[b]	Ohio		Short	J. Ross, E. Bridge, M. Rozmarynowycz, and V. Bingman (unpubl.)
Bicknell's Thrush (*Catharus bicknelli*)	4,44	4/45 (9%)	-	USA – 3 sites		Short	Renfrew *et al.*, in press

Bicknell's Thrush	3,33	13/60 (22%)	-	USA – 3 sites		Short	Renfrew *et al.*, in press
Northern Wheatear (*Oenanthe oenanthe*)	5	2/16 (13%)	2/33 (6%)	Nunavut		Long	Bairlein *et al.*, 2012
Red-backed Shrike (*Lanius collurio*)	3,67	26/151 (17%)	(24%-37%)[a]	Scandinavia		Long	Šimek 2001, pasinelli *et al.*, 2007, Tøttrup *et al.*. 2011
Swainson's Thrush (*Catharus ustulatus*)	3,55 – 3,87	10/39 (26%)	(~36%)[a]	Britisch Colombia		Medium	Evans *et al.*, 1998, Delmore *et al.*, 2012
Fork-tailed Flycatcher (*Tyrannus savana*)	2,9 – 3,87	9/44 (20%)	N/A	Argentina		Short	A.Jahn, V. Cueto, D. Tuero, D. Levey, and D. Masson (unpubl.)
Fork-tailed Flycatcher	3,75	0/15 (0%)	N/A	Bolivia		Short	A.Jahn, d. Levey, and A. Mamani, (unpubl.)

Golden-crowned Sparrow (*Zonotrichia atricapilla*)	3,33	11/33 (33%)[d]	11/28 (39%)	California		Short	Seavy *et al.*, 2012
Veery (*Catharus fuscescens*)	4,2857	16/24 (67%)[e]	(62%)[g]	Delaware		Medium	Heckscher *et al.*, 2011
Snow Bunting (*Plectrophenax nivalis*)	3,15	13/90 (14%)	N/A	Nunavut		Medium	Macdonals *et al.*, 2012
Grey Catbird (*Dumetella carolinensis*)	4,44	7/22 (32%)	88/294 (30%)	Maryland		Short	Ryder *et al.*, 2011
Scissor-tailed Flycatcher (*Tyrannus forficatus*)	2,5	5/38 (13%)	1/3 (33%)[g]	Oklahoma		Short	A.Jahn, M.Husak, D. Landoll, and J. Fox, (unpubl.)
Eastern Kingbird (*Tyrannus tyrannus*)	2,432	1/2 (50%)	N/A	Oklahoma		medium	A.Jahn, M.Husak, D. Landoll, and J. Fox, (unpubl.)

Tropical Kingbird (*Tyrannus melancholicus*)	2,093 – 2,79	1/5 (20%)	1/1 (100%)[g]	Argentina		Short	A.Jahn, V. Cueto, D. Tuero, D. Levey, and D. Masson (unpubl.)
White-throated Kingbird (*Tyrannus albogularis*)	3	2/8 (25%)	1/5 (20%)	Bolivia		Short	A.Jahn, D. Levey, O. Barroso, and A. Mamani, (unpubl.)
Western Kingbird (*Tyrannus verticalis*)	2,25	16/40 (40%)	3/9 (33%)	Oklahoma		Short	A.Jahn, M. Husk, D. Landoll, and J. Fox, (unpubl.)
Common Swift	3,02	6/8 (75%)	(~80%)[a]	Sweden		Long	Perrins 1971, Akesson *et al.*, 2012
Purple Martin (*Progne subis*)	1,6667	3/6 (50%)	N/A	Oklahoma		Long	E. Birdge and J. Kelly (unpubl.)
Purple Martin	3,06	2/18 (11%)	137/330 (41%)	Pennsylvania		Long	Stutchbury and J.Kelly (unpubl.)
Purple Martin	2,2449	3/16 (19%)	93/255 (36%)	Pennsylvania	Same	Long	Stutchbury, unpubl.

Purple Martin	2,245	39/87 (45%)	104/341 (35%)	Pennsylvania	Same	Long	K. Fraser and B. Stutchbury, unpubl.
Wood Thrush (*Hylocichla mustelina*)	3	37/97 (38%)	29/111 (26%)	Pennsylvania		Medium	Stutchbury et al. 2009; C.Stanley, E. McKinnon, K. Fraser, M. MacPherson, and B. Stutchbury (unpubl.)
Wood Thrush	3	25/109 (23%)	7/100 (7%)	Costa Rica		Short	C. Stanley, E. McKinnon, K. Fraser, M. MacPherson, and B. Stutchbury (unpubl.)
Wood Thrush	3	10/73 (14%)	9/78 (12%)	Belize		Short	C. Stanley, E. McKinnon, K. Fraser, M. MacPherson, and B. Stutchbury (unpubl.)
Northern Black Swift (*Cypseloides niger borealis*)	2,35	3/4 (75%)	(41%)[f]	Colorado		Short	Beason *et al.*, 2012
European Bee-eater (*Merops apiaster*)	1,85	5/40 (13%)	20/40 (50%)	Germany		Medium	Arbeiter *et al.*, 2012
Rusty Blackbird (*Euphagus carolinus*)	3,64	3/17 (18%)	(60%)[b]	Alaska		Medium	Johnson *et al.*, 2012

Yellow-billed Cuckoo (*Coccyzus americanus*)	2,5	1/13 (8%)	5/52 (10%)[a]	New mexico		Medium	Halterman 2009, Sechrist *et al*., 2012
Hoopoe (*Upupa epops*)	2,57	5/19 (26%)	25/111 (23%)	Switserland		Short	Bächler *et al*., 2010
American Robin (*Turdus migratorius*)	2,25	10/37 (27%)	3/11 (27%)	Kentucky		Short	D. Brown (unpubl.)

[a] From a previous and separate study.
[b] From previous year or years.
[c] Recaptured on wintering grounds during same year as deployment.
[d] Seven of the returned birds lost their tags.
[e] Nine of the returned birds lost their tags
[f] Multi-year average.
[g] Sample too small for valid comparison