TRACKING HUMMINGBIRD FORAGING MOVEMENTS AND PATCH-USE IN THE WILD WITH PASSIVE INTEGRATED TRANSPONDERS

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ABSTRACT

We show how PIT tags can be glued on the back of Ruby-throated Hummingbirds (*Archilocus colubris*). Using this method, we were able to track free-ranging, adult hummingbirds within a 44-ha grid composed of 45 artificial feeders equipped with PIT-tag readers for a mean (± SD) of 25.7 ± 22.1 days (median = 19 days, max = 95 days; *n* = 253). Over 4 years, we tracked 253 individuals that provided 8,199,503 PIT-tag readings during 238,316 visits to feeders. Although tag retention time was not affected by the amount of precipitations that fell within 3 days from tagging, the hazard of loosing a tag was 6.9 times higher for females than for males. We also contrast yearly recapture rates of individuals over 4 years at 2 sites spaced by 33 km: our main study site (band + PIT tag; *n* = 253) and one where adult hummingbirds were fitted only with a leg band (*n* = 508). Apparent survival differed between sexes, but not across sites. Moreover, PIT-tagged hummingbirds had a yearly recapture rate 1.5 times higher than that of hummingbirds carrying only a leg band (males: 63% vs 40%; females: 67% vs 40%). Although treatment was confounded with site in our analysis, our results suggest that 3.5-g hummingbirds can carry a PIT tag glued on their back without incurring major costs. Based on a sample of the information we obtained, we maintain that PIT tags offer research opportunities of untapped proportions with regard to the spatially-explicit, foraging ecology of small bird species that strongly depend on localized food sources.

Key words: hummingbirds, passive integrated transponders, pit tags, foraging movement, patch use, patch residence time.

Direct observation rarely allows to determine precisely what wild animals do as well as when and where they do it over a long timeframe or over a large spatial scale. Notwithstanding the inherent difficulty of detecting individuals, this is particularly true when dealing with vagile species such as birds. Ornithologists have partially overcome this problem by coupling sophisticated tracking devices (e.g., GPS-platform terminal transmitters) with environmental or physiological data loggers (e.g., time-depth, stomach-temperature or jaw-movement recorders), which provide information on when and where birds forage and catch prey (reviewed by Ropert-Coudert and Wilson 2005, Burger and Shaffer 2008). In spite of significant advances at miniaturizing bio-logging devices, their use remains restricted to large species, such as seabirds (Burger and Shaffer 2008). Hence, researchers must often rely on imprecise, low-range or short-life tracking devices (e.g., VHF radio tags, harmonic radar) and their eyes to address the spatial, behavioral ecology of passerines and smaller birds (e.g., Evans et al. 2008). For instance, the smallest VHF radio tags currently available (ca. 0.2 g; Naef-Denzer et al. 2005) have been used to track the homing movements of translocated, large hummingbirds (>5.5g; Hadley and Betts 2009). Yet, two teams of observers with radio receivers and handheld Yagi antennae had to follow by foot the marked birds and this within 200 m in order to obtain locations with 50-m accuracy.

One technology that circumvents the problems of weight, size, and durability of devices is radio frequency identification (RFID) using passive integrated transponders, better known as PIT tags (reviewed by Gibbons and Andrews 2004). PIT tags devoted to biological use usually consist of an electronic microchip embedded in biocompatible glass. When activated by an electromagnetic field, the tag sends back a signal that codes for a unique alphanumeric ID. PIT tags can be as big or smaller than grains of rice because the energy source required to activate the tags comes from the reading device and not from a battery that must be carried by the animal.

This small size also allows to embed the tag under the skin in muscle or the body cavity or to glue it to leg bands, for example. Unfortunately, those advantages come at the cost of a detection range that varies from a few millimeters for the smallest tags to less than a meter for the largest ones. PIT-tag technology was first utilized with wild birds of large size (e.g., penguins; Le Maho and Gendner 1993), and is now being used with small birds to monitor, for instance, nest attendance or visits (e.g., plovers, wrynecks and flycatchers; Freitag et al. 2001, Ottosson et al. 2001, Kosztolànyi and Székely 2002). It has also been used to monitor patch use or selection in a foraging context with captive birds (e.g., starlings and juncos; Vézina et al. 2001, Olsson et al. 2002). To our knowledge, PIT tags have never been used specifically to track the movements of individuals among specific locations, such as feeding sites, but only opportunistically with migrating storks (Michard et al. 1995).

Here, we detail how PIT tags can be fitted to one of the smallest bird species, the Ruby-throated Hummingbird (*Archilocus colubris*), in order to address various aspects of its spatial ecology. We also provide data on tag retention by free-ranging hummingbirds evolving within a 44-ha grid composed of 45 artificial feeders. Given that our method involves the glueing of a PIT tag to the back feathers of individuals, we quantify the effect of precipitations and investigate if attributes linked to the sex of individuals, such as differential body size and habitat use, have a bearing on tag retention. We further contrast the yearly recapture rates of individuals at two geographically-close banding sites, our main study site (band + PIT) and one where hummingbirds are fitted only with a leg band, in order to provide a crude estimation of the influence of glueing a PIT tag on individuals. Lastly, we provide a brief overview of the research possibilities offered by PIT tags using our database on hummingbird foraging movements. Specifically, we present data on the duration of visits to feeders, the time elapsed between visits at feeders, the number of feeders visited during one day, and contrasting, spatially-explicit movement paths of foraging individuals. We believe that PIT tags offer research opportunities of untapped proportions with regard to the spatially-explicit, foraging ecology of small, nectarivore birds and of other bird species which strongly depend on localized food sources. Indeed, one can thereby monitor the visits made by a large number of individuals over a large array of (experimental) feeding sites during an extensive time period with great accuracy and minimum observer effort.

METHODS

Study area and experimental design

We captured and marked Ruby-throated Hummingbirds to monitor their foraging movements between 20 May and 30 August 2006-2009 on a 44-ha grid composed of 45 artificial feeders located in Cleveland County, Quebec, Canada (45°, 40' N; 72°, 05' W; Fig. 1; hereafter referred to as our main study site). Feeders (Yule Hide, model HB81, capacity: 455 ml) were spaced by 100 m and mounted on a metal pole 1.5 m above ground with an angle bracket (Fig. 2). We covered feeders with an olive-painted, aluminum plate (diameter: 60 cm) fitted to the angle bracket to limit direct sun exposure which increases nectar evaporation and thereby nectar sucrose concentration. A funnel filled with water enveloped the pole 0.5 m above ground in order to prevent ants to access the feeder. We cleaned and replaced feeders each week. Feeders were (generally) filled with a fresh solution of 20% (w/v) sucrose. This mixture is similar in composition to the nectar found in the flowers visited by wild hummingbirds (Baker 1975, Bolten et al. 1979, Chalcoff et al. 2008).

The base of feeders was red in color and originally contained four yellow 'flowers' equipped with a small perch from which hummingbirds could drink. We removed three of the four flowers and perches to force hummingbirds to visit a single flower. The antenna of the PIT-tag reader, which consisted in a rectangular, single coil (Trovan Ltd., UK, model LID650, model ANT 614 OEM; 5 x 8 cm), was attached to the perch of this single flower with 2 tie wraps (Fig. 2). The other end of the antenna was hooked to a PIT-tag reader (Trovan Ltd., UK, model LID650) powered by a 12-V battery which lasted 90 days under field conditions. Readers were programmed to scan for PIT tags every second and record the PIT tag ID, date, and time (hour, min, sec) if detected using the LID650/LID665/LID1260 software (Trovan Ltd., UK, version 703). Readers had a capacity of 6500 entries and had to be more or less frequently downloaded using a portable computer equipped with a serial port and the LID650/LID665/LID1260 software.

Capturing and banding hummingbirds

We captured hummingbirds with mist nets (mesh size: 25 mm) and Hall traps (Russell and Russell 2001). Once individuals were fitted with an official, aluminum leg band (size X), we noted their body mass (± 0.1 g), wing chord (± 1 mm), exposed culmen length (± 1 mm), as well as their sex and age following Pyle (1997), and the number of mallophaga found in their throat feathers. We then colored the breast of hummingbirds with a non-toxic, permanent marker for visual identification (Russell and Russell 2001). We allowed hummingbirds to drink nectar from an artificial feeder every 2-5 min throughout the manipulations, including glueing the PIT tag (see below).

Fitting PIT tags on hummingbirds

We used one of the smallest PIT tags available on the market that had a minimal detection range of 2.5 cm given our reading devices (Trovan Ltd., UK, model ID100A; weight: 0.09 g; size: 2.12 x 11.50 mm). The tag, the glue (see below), and the leg band weighed on average less than 5% of the hummingbirds' body mass (i.e., ca. 0.12 g; male body mass (mean ± SD) = 2.93 ± 0.40 g, n = 183; female body mass = 3.52 ± 0.66 g, n = 194). This amount of weight is acceptable according to established standards (e.g., White and Garrott 1990).

Before glueing PIT tags to the back of hummingbirds, we placed them into an indented piece of foam such that the back of the birds was fully accessible and their wings kept immobile with just enough pressure (Fig. 3). This allowed us to work with both hands and thereby benefit from a greater dexterity. Using tweezers, we first put a single drop of hypo-allergenic, nail glue made of ethylcyanoacrylate (Sally Hansen, USA, no. 2213) on the tag before placing it along the longitudinal axis of the body in the interscapular region (Fig. 3). This first step is crucial given that there is only one opportunity to lodge the tag in the right place, inasmuch as this must be done before the glue dries up (i.e., < 3 sec). In order to secure the tag in place and protect the nail glue bonding, we added a small coat of surgical glue (Torbot Group, Inc., USA, Liquid Bonding Cement, no. TT410) on the tag periphery. The surface of the surgical glue dried within 10 sec. It is extremely important to avoid spilling glue on the scapulars since this may impair flight. All the above manipulations (i.e., banding, measuring, tagging) took less than 10 min.

Statistical analyses

We assessed the influence of precipitations and of the sex of individuals on tag retention time using proportional hazards models, better known as Cox regressions (Therneau and Grambsch 2000). Tag retention time was defined as the time elapsed between tagging and the last detection of a given tag ID by RFID on our study area. Although tag retention time could be estimated for individuals that were recaptured by hand without their tag, it could not be estimated for individuals that were not recaptured in that manner. Indeed, some individuals may have died, lost their tag, or left the study area without having lost their tag. Hence the time elapsed until the last detection of such individuals had to be treated as random, right-censored data (Allison 1995). Given that those conditions (e.g., leaving the study site) should have no bearing on the likelihood of loosing a tag, we assumed that the censored data were uninformative with respect to tag retention time and thus appropriate for standard Cox regression methods (Allison 1995).

We used a backward variable selection procedure starting with a model that contained the amount of precipitations (mm; measured *in situ* with a pluviometer) that fell in the three days that followed tagging, the sex of the individual, and their interaction. We focused on these three variables because rain can reduce the adhesive properties of the glues and lead birds to increase their preening and grooming activities, thereby increasing the likelihood of tag removal. Differences in tag retention across sex may occur as females are larger than males, have longer beaks, and thus are likely more apt at physically removing tags. Moreover, males spend much more time than females in open habitat, and thus are potentially exposed to direct rain (Y. Charette, F. Rousseu, and M. Bélisle., unpubl. data). Yet, females may suffer from a greater exposure to rain than males as the former is the only sex that incubates and broods. These difference in body size and behavior linked to sex warranted the inclusion of the precipitation by sex interaction.

We assessed the significance of regression parameters with the likelihood-ratio statistic based on maximum partial likelihood estimates calculated by the Exact method (Therneau and Grambsch 2000). The alpha level was fixed at 0.05. Models were fitted using the coxph function of the survival package (version 2.35-8, Therneau 2009) run in R 2.10.1 (R Development Core Team 2009).

Lastly, we used a mark-recapture approach to determine whether hummingbird apparent survival (φ) and recapture probability (p) differed between hummingbirds fitted with a leg band

and a PIT tag (main study site: feeder grid in Cleveland County) or only with a leg band (site: Stoke, Quebec; 45°, 32' N; 71°, 48' W; 33 km from main study site), as well as across sexes. Because the juvenile data were sparse, we only considered adult capture histories to estimate the parameters under the Cormack-Jolly-Seber model (Lebreton et al. 1992, Williams et al. 2002). We considered a total of 17 candidate models, contrasting 4 different hypotheses on apparent survival and recapture probabilities (Table 2). We computed maximum likelihood estimates of the survival and recapture parameters for each model with Mark 5.1 (White and Burnham 1999). Our global model, $\varphi_{site*sex*t}$ $p_{site*sex*t}$, assumed time-dependent apparent survival and recapture for each sex at each site. We used the global model to test goodness-of-fit. None of the goodness-of-fit tests implemented in U-CARE 2.2 revealed systematic departures from model assumptions (Choquet et al. 2005). Neither the bootstrap $\hat{c}$ nor the median $\hat{c}$ approaches suggested the presence of overdispersion with estimates of 0.89 (from 10 000 samples) and 0.98 (from 12 groups of 10 samples), respectively. We ranked the models based on the AIC_c and performed multimodel inference on the parameter estimates following Burnham and Anderson (2002).

RESULTS

We only considered adult Ruby-throated Hummingbirds captured between 20 May and 31 July to limit the inclusion of migrating individuals in our sample. During this period, we tagged 49, 77, 64, and 63 individuals in 2006, 2007, 2008, and 2009, respectively. Tracking those individuals lead to 8,199,503 PIT-tag readings over the 4 years. Assuming that readings had to be spaced by more than 20 sec to be considered as pertaining to subsequent visits to a given feeder, these readings characterized 238,316 different visits to feeders.

We tracked tagged individuals for a mean (± SD) of 25.7 ± 22.1 days, the maximum being 95 days (median = 19 days; n = 253). Tag retention time was not affected by the amount of precipitations that fell in the 3 days following tagging. However, females had lower retention times than males, as the hazard of loosing a tag was 6.9 times higher for females than for males (Table 1, Fig. 4).

Lastly, the model consisting of sex-dependent apparent survival and site-dependent recapture probability $\varphi_{sex}\, p_{site}$ ranked highest among our candidate models with an Akaike weight of 0.61 (Table 2). This model was 6.1 times more parsimonious than the second-ranked model, $\varphi_{sex}\, p_{site*sex}$, which assumed sex-dependent survival and different recapture probabilities for each sex and site combinations. Model-averaging indicated that apparent survival differed between sexes, but not across sites. In both sites, females experienced an apparent survival rate 1.6 times higher than that of males (Table 3). Model-averaging also revealed that the hummingbirds we banded and tagged on our main study site (feeder grid) had a recapture rate that was 1.5 times higher than that of hummingbirds that were only banded in Stoke (Table 3).

DISCUSSION

We described an easy and efficient method to fit PIT tags on the back of Ruby-throated Hummingbirds in the field. Indeed, we showed that PIT tags can be glued at low cost to hummingbirds in less than 10 min and provide tremendous amounts of detailed data on the concurrent spatio-temporal, foraging habits of numerous individuals for several days, even months (Figs. 5 and 6). Moreover, our method did not seem to affect negatively the survival of the hummingbirds, nor their philopatry as estimated through recapture rate.

Female Ruby-throated Hummingbirds lost their tags more rapidly than males. We attribute this difference to the larger body size of females. Being larger and having longer beaks, females are likely better equipped than males to remove tags. Yet, we cannot dismiss the fact that male and female Ruby-throated Hummingbirds also differ in their habitat use and behavior. Males are most often found in open habitat, whereas females occur mostly in forested regions of our study area and only females incubate and brood (Robinson et al. 1996). Such differences may affect the bonding quality of the glues through variation in exposure to weather elements, for instance. In contrast to our prediction, however, the amount of precipitations that fell in the 3 days that followed tagging did not affect tag retention time. We nevertheless believe that embedding the tag in the plumage instead of putting it on the plumage surface will be a great improvement once PIT-tag miniaturizing reaches new levels. This should reduce both glue and tag exposure to weather elements and increase retention time.

Although miniaturization of tracking devices certainly reduces their negative impact on the health and behavior of birds (Burger and Shaffer 2008), current PIT-tag technology seems already appropriate to mark even the smallest (long-distance) migrating birds. Indeed, we did not find any difference in apparent survival nor recapture probability between Ruby-throated Hummingbirds fitted with both a leg band and a PIT tag and those fitted solely with a leg band (Table 3). We stress, however, that our results cannot support a firm conclusion with respect to the impact of glueing a PIT tag on the back of hummingbirds of the size of Ruby-throated Hummingbirds because our analysis was afflicted by pseudoreplication (i.e., carrying or not a PIT tag was confounded with study sites). Nevertheless, our mark-recapture analysis coupled to the fact that we never observed a tagged hummingbird trying to remove its tag or preening its back intensively, and this in spite of >5000 hours of field work, lead us to believe that PIT tags do not have a strong impact on hummingbirds (compared to passerines carrying a radio transmitter, for instance). Moreover, hummingbirds experience daily and seasonal variations in body mass that are much more important than the additional weight implied by a glued PIT tag (e.g., Norris et al. 1957, Hiebert 1991).

Because PIT tags are glued on feathers, hatching-year and after-hatching-year Ruby-throated hummingbirds lost their tags at the latest during their pre-basic molt, which occurs between October and April according to Pyle (1997) but can start as soon as August on our study area (Charette, unpl. data). Such an extensive molt period limits the possibilities of following the migration patterns or the movements of this species on its wintering grounds. It also forces researchers to recapture birds at least once a year in order to follow individuals across years. Nevertheless, recapturing birds across years is possible, at least on their breeding grounds, as we were able to tag 48 individuals on 2 consecutive years, 9 on 3 consecutive years, and 2 on 4 consecutive years (n = 302 birds across 2006-2009; sample includes birds of both sexes and all ages, irrespective of capture date). Another constraint of our method lies in the costs of acquiring PIT tag readers. One reader and its associated equipment (e.g., 12-V battery, feeder) cost us ca. 800$ US in 2005. Once equipped, operational fees are, however, mostly related to salaries and travel as data from readers may have to be uploaded every day.

The research potential stemming from the use of PIT tags with birds attracted to specific locations, such as food sources, is tremendous and unique with respect to small birds. Monitoring the movements and space use of a large number of PIT-tagged individuals simultaneously over relatively large spatial and temporal scales, now enables researchers to address timely questions regarding resource monopolization and defense, territoriality, habitat selection, and foraging strategies. For instance, PIT tags could definitely help quantify the level of traplining used by wild hummingbirds within and across species under different ecological conditions. Indeed, nectarivorous birds, such as hummingbirds, that do not defend renewable food sources (e.g., flowers) have been hypothesized to trapline in order to maximize nectar intake while minimizing nectar loss to competitors (Gill 1988). Yet, most (if not all) accounts of traplining in wild hummingbirds are based on assessments of regular visits by (un)marked individuals at a single, focal food patch (e.g., Garrisson 1995, Gill 1988, Temeles et al. 2006). By focusing on the moments at which marked individuals visited a single food patch, studies that documented traplining in wild hummingbirds have totally neglected the spatial component of this foraging strategy. PIT tags provide the information necessary to quantify traplining levels of wild hummingbirds in both space and time.

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Table 1. Variable selection for PIT-tag retention time by adult Ruby-throated Hummingbirds marked between 20 May and 31 July 2006-2009 in Cleveland County, Quebec, Canada (n = 253). A backward selection procedure was applied to a model that contained the amount of precipitations (mm) that fell in the three days that followed tagging, the sex of the individual, and their interaction. Note that we are showing the three elimination iterations leading to the final model (model 3). Models were fitted by Cox regression (see Methods for details). Significance of parameters based on a likelihood-ratio test (LRT). Reference category for sex is male. Hazard ratios are found under Exp(β).

Model	Variable	β	SE	Exp(β)	LRT	*P*
1	sex (female)	1.72	0.59	5.56	9.83	0.002
1	precipitations	-0.02	0.03	0.98	0.39	0.53
1	sex x precipitations	0.02	0.03	1.02	0.33	0.56
2	sex (female)	1.94	0.47	6.94	20.96	<0.001
2	precipitation	0.00	0.01	1.00	0.05	0.82
3	sex (female)	1.93	0.47	6.90	20.92	<0.001

Table 2. Model selection based on the AIC_c for Cormack-Jolly-Seber models estimating adult Ruby-throated Hummingbird apparent survival (φ) and recapture probability (p). Birds were marked in summer between 2006-2009 in Cleveland County (leg band + PIT tag, n = 253) and Stoke (leg band only, n = 508), Quebec, Canada. Model notation follows that of Lebreton et al. (1992) and indices denote the constraints on survival and recapture. For instance, $\varphi.$ indicates constant survival, whereas $\varphi_{site*sex}$ corresponds to a different survival estimate for each sex at each site.

Model	Number of parameters	AIC_c	Delta AIC_c	Akaike weight
$\varphi_{sex}\ p_{site}$	4	674.14	0	0.61
$\varphi_{sex}\ p_{site*sex}$	6	677.76	3.62	0.10
$\varphi_{site*sex}\ p_{site}$	6	678.15	4.01	0.08
$\varphi_{.}\ p_{site*sex}$	5	679.28	5.14	0.05
$\varphi_{site*sex}\ p_{.}$	5	679.51	5.37	0.04
$\varphi_{site*sex}\ p_{site*sex}$	8	679.6	5.46	0.04
$\varphi_{site}\ p_{sex}$	4	681.13	6.99	0.02
$\varphi_{site}\ p_{site*sex}$	6	681.31	7.17	0.02
$\varphi_{site*sex}\ p_{sex}$	6	681.52	7.38	0.02
$\varphi_{sex}\ p_{.}$	3	681.94	7.80	0.01
$\varphi_{sex}\ p_{sex}$	4	683.95	9.82	0
$\varphi_{.}\ p_{site}$	3	684.23	10.09	0
$\varphi_{.}\ p_{sex}$	3	685.89	11.76	0
$\varphi_{site}\ p_{site}$	4	686.25	12.11	0
$\varphi_{site}\ p_{.}$	3	687.93	13.79	0
$\varphi_{site*sex*t}\ p_{site*sex*t}$	20	691.35	17.22	0
$\varphi_{.}\ \mathrm{p}_{.}$	2	695.87	21.73	0

Table 3. Model-averaged estimates of apparent survival (φ) and recapture probability (p) of adult Ruby-throated Hummingbirds marked in summer between 2006-2009 in Cleveland County (leg band + PIT tag, n = 253) and Stoke (leg band only, n = 508), Quebec, Canada. Estimates are based on entire set of candidate models (Table 2). Note that 95% unconditional confidence limits were computed on the logit scale and then back-transformed.

Type	Sex	Site	Model-averaged estimate	Unconditional SE	Lower 95% confidence limit	Upper 95% confidence limit
Apparent survival	Female	Stoke	0.418	0.074	0.283	0.566
Apparent survival	Male	Stoke	0.254	0.063	0.150	0.396
Apparent survival	Female	Richmond	0.421	0.057	0.314	0.536
Apparent survival	Male	Richmond	0.268	0.065	0.161	0.413
Recapture	Female	Stoke	0.400	0.099	0.230	0.599
Recapture	Male	Stoke	0.404	0.123	0.200	0.649
Recapture	Female	Richmond	0.673	0.113	0.431	0.849
Recapture	Male	Richmond	0.631	0.143	0.339	0.850

FIGURE LEGENDS

Figure 1. Main study area consisting of a 44-ha grid composed of 45 artificial feeders, each equipped with a PIT-tag reader, and located in Cleveland County, Quebec, Canada. Feeders (black dots) were spaced by 100 m.

Figure 2. A feeder equipped with its PIT-tag reader and antenna. The reader was powered by a 12-V battery. A serial port was hooked to the reader for downloading data. The aluminum plate limited exposure to sun and rain and the funnel filled with water prevented ants from gaining access to nectar. See Methods for details.

Figure 3. Adult female Ruby-throated Hummingbird placed in an indented piece of soft foam in order to keep its wings immobile and give full access to its back for glueing the PIT tag. The tag on the picture is held in place with hypo-allergenic nail glue. Note that we added a small coat of surgical glue on the tag periphery to secure the tag in place and protect the nail glue bonding.

Figure 4. PIT-tag retention time by adult Ruby-throated Hummingbirds marked between 20 May and 31 July 2006-2009 in Cleveland County, Quebec, Canada (n = 253). Survival curves for both sexes were computed using a Cox regression with sex as an explanatory variable (See Methods and Table 1). Crosses depict censured data points.

Figure 5. Examples of data gathered on 26 July 2008 with Ruby-throated Hummingbirds fitted with PIT tags and roaming on a 44-ha grid composed of 45 artificial feeders equipped with PIT-

tag readers (See Figure 1). The first 2 histograms are from an adult female tracked for 90 days in 2008 and the last 2 are from 36 individuals detected on the feeder grid on the same day. A) Visit durations at the most visited feeder on that day. B) Intervisit durations at the most visited feeder on that day. C) Number of different feeders visited by every individual detected. D) Spatial concentration of individuals in relation to feeder rank. Spatial concentration consists in the ratio between the number of visits made at a particular feeder by a given individual and the total number of visits made to feeders by that individual on a given day. Feeders have been ranked for every detected individual from the most (rank 1) to the least visited. The absence of data beyond certain ranks in panel D is explained by the fact that some feeders share the same rank because of an equal number of visits.

Figure 6. Spatial pattern of visits to feeders made by an adult female Ruby-throated Hummingbird on 26 July 2008 within a 44-ha grid composed of 45 artificial feeders equipped with PIT-tag readers (See Figure 1). This PIT-tagged hummingbird was followed for 90 days in 2008. Small dots depict unused feeders while large dots identify visited feeders. Large numbers indicate the number of visits and small numbers the number of movements recorded between feeders, without distinction of movement direction. The northern section of the feeder grid is not shown for convenience.

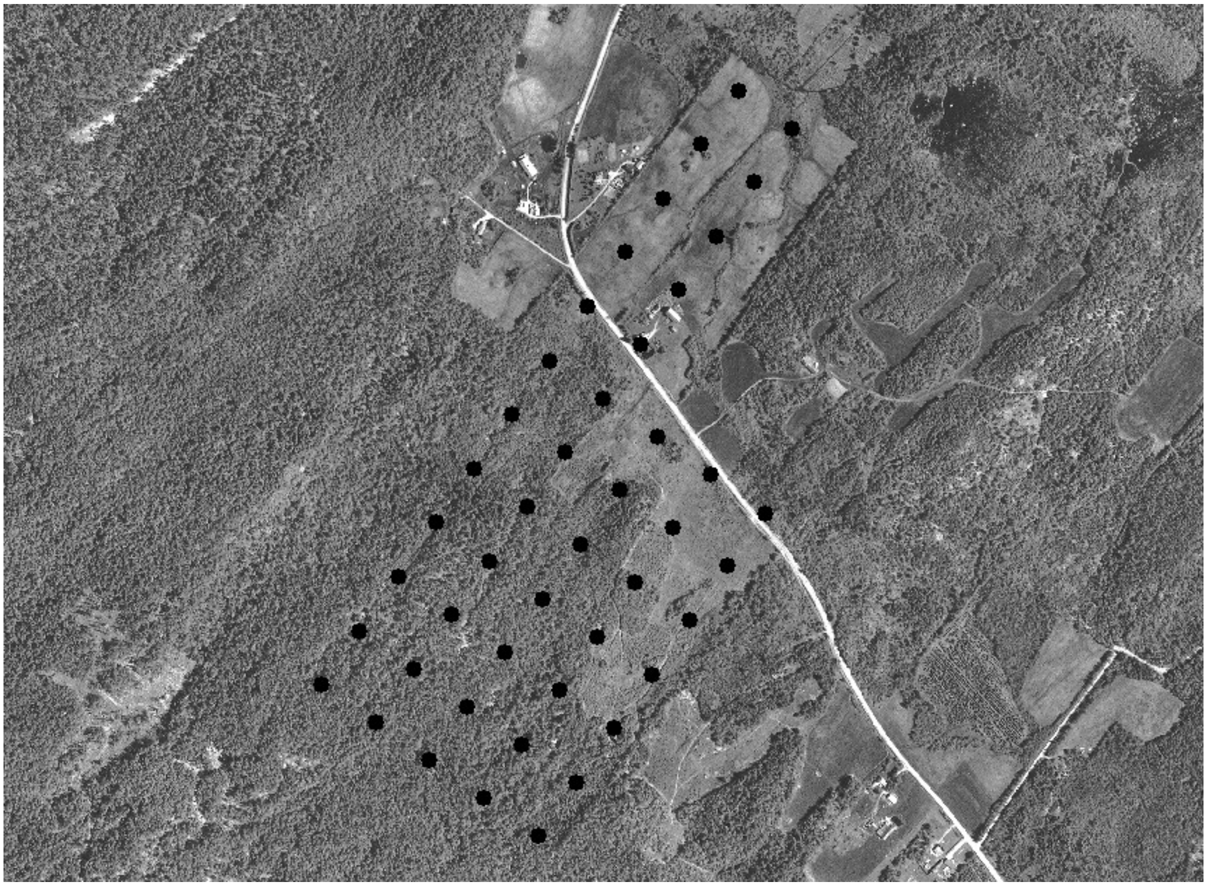

Figure 1.

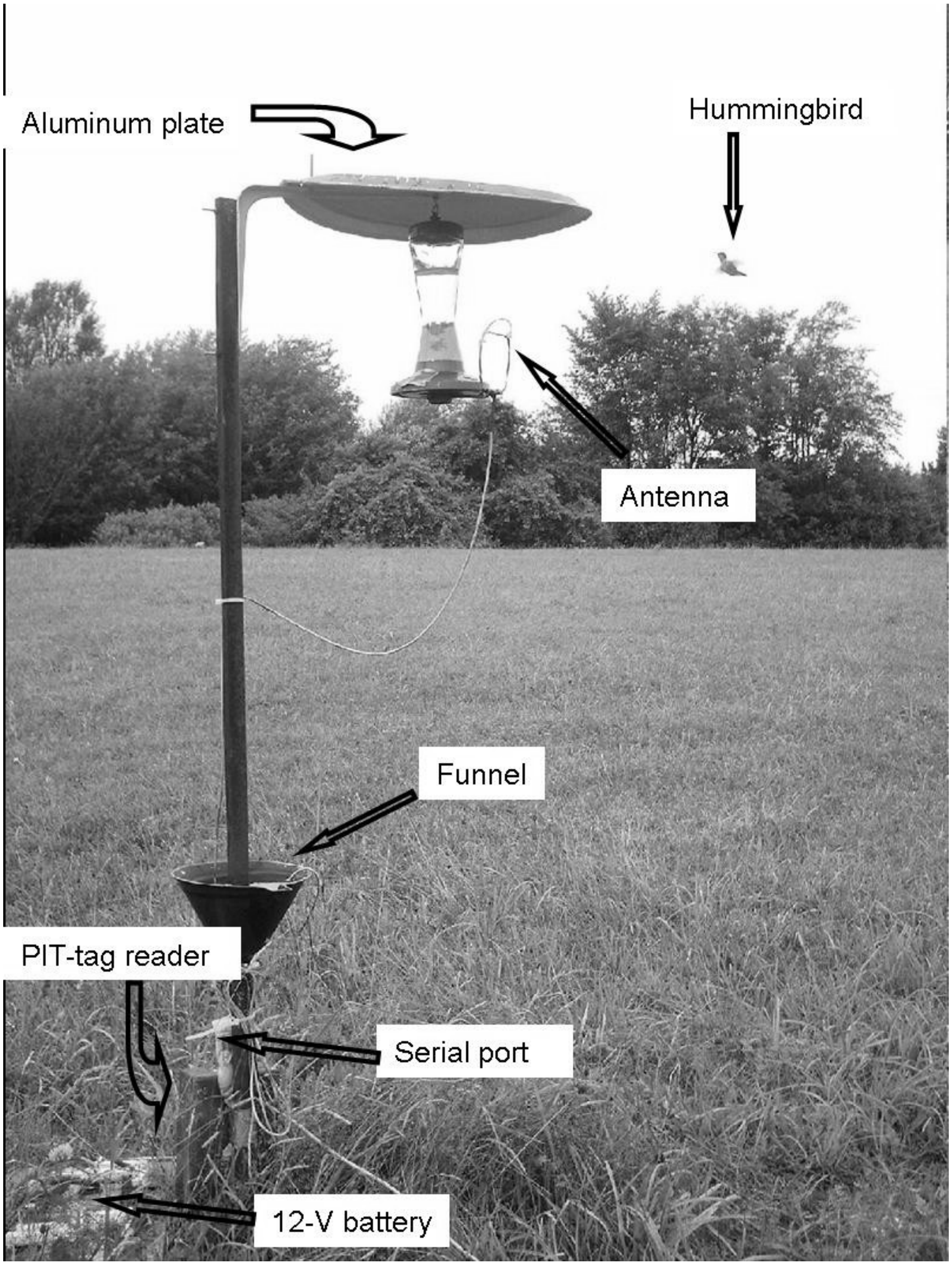
Aluminum plate
Hummingbird
Antenna
Funnel
PIT-tag reader
Serial port
12-V battery

Figure 2.

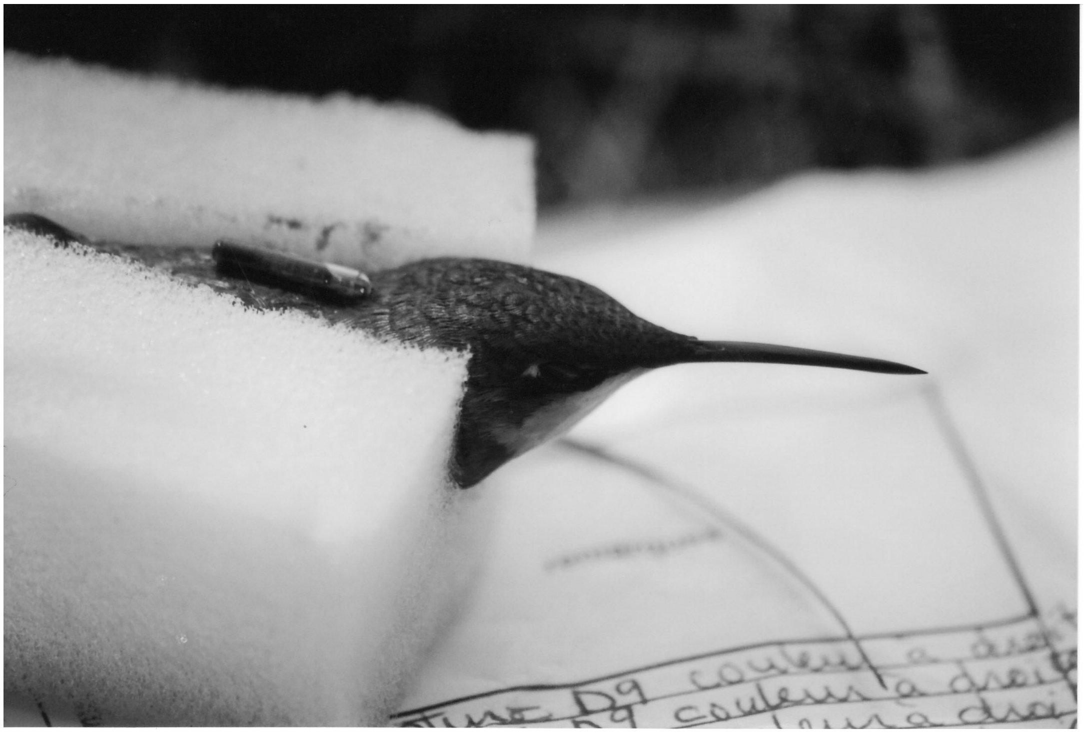

Figure 3.

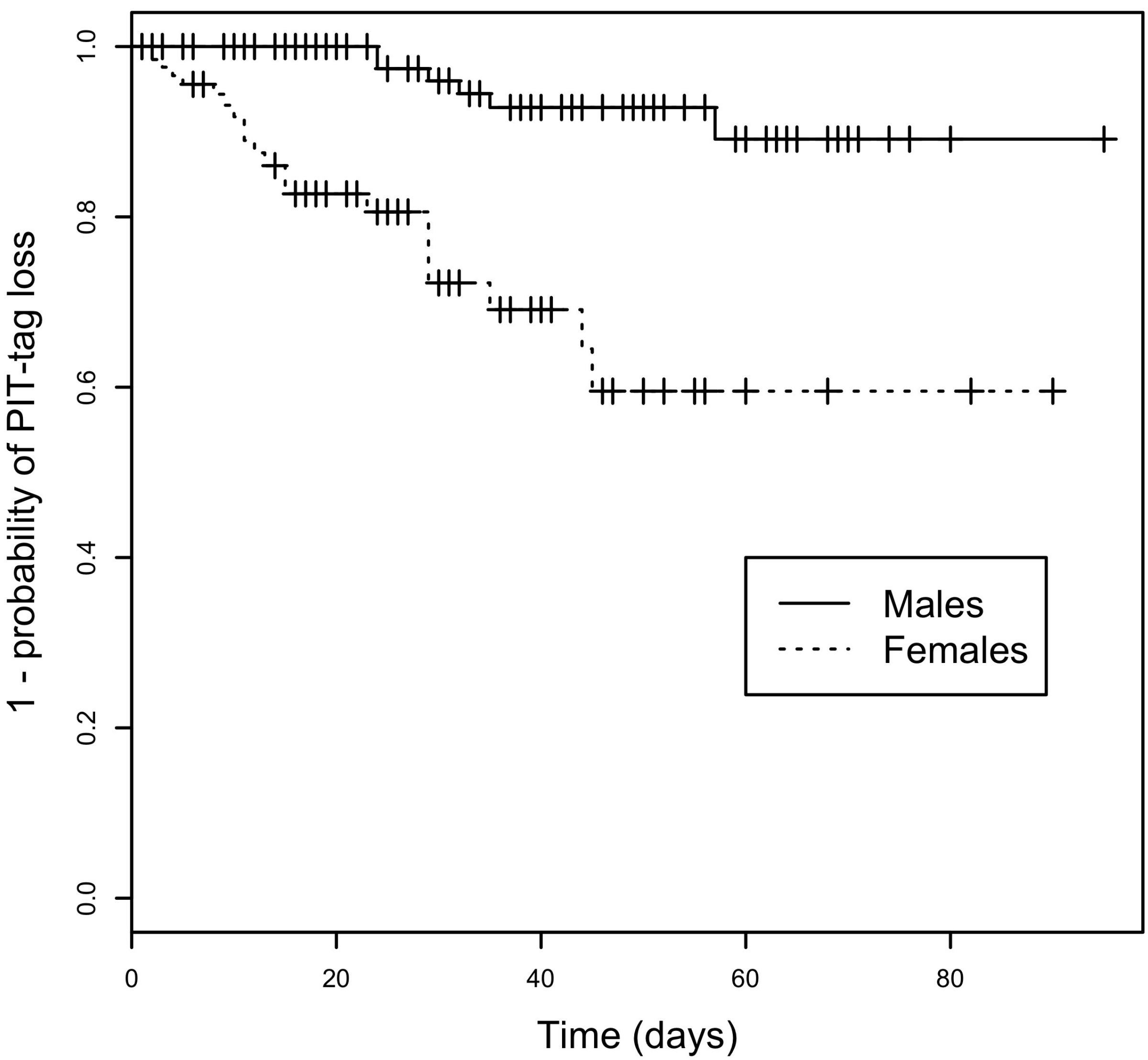
1 - probability of PIT-tag loss
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
Time (days)
Males
Females

Figure 4.

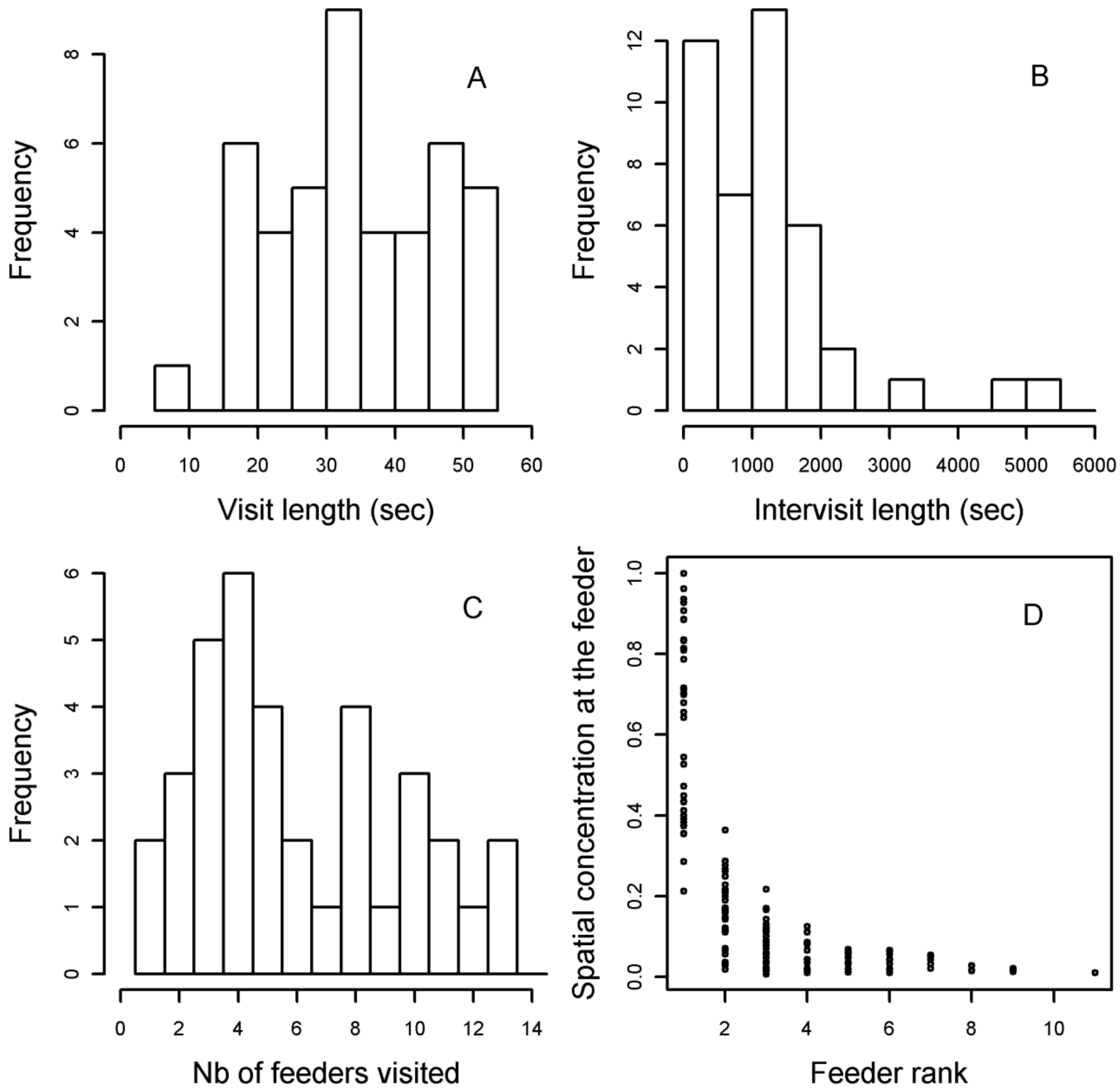
A
Frequency
Visit length (sec)
B
Frequency
Intervisit length (sec)
C
Frequency
Nb of feeders visited
D
Spatial concentration at the feeder
Feeder rank

Figure 5.

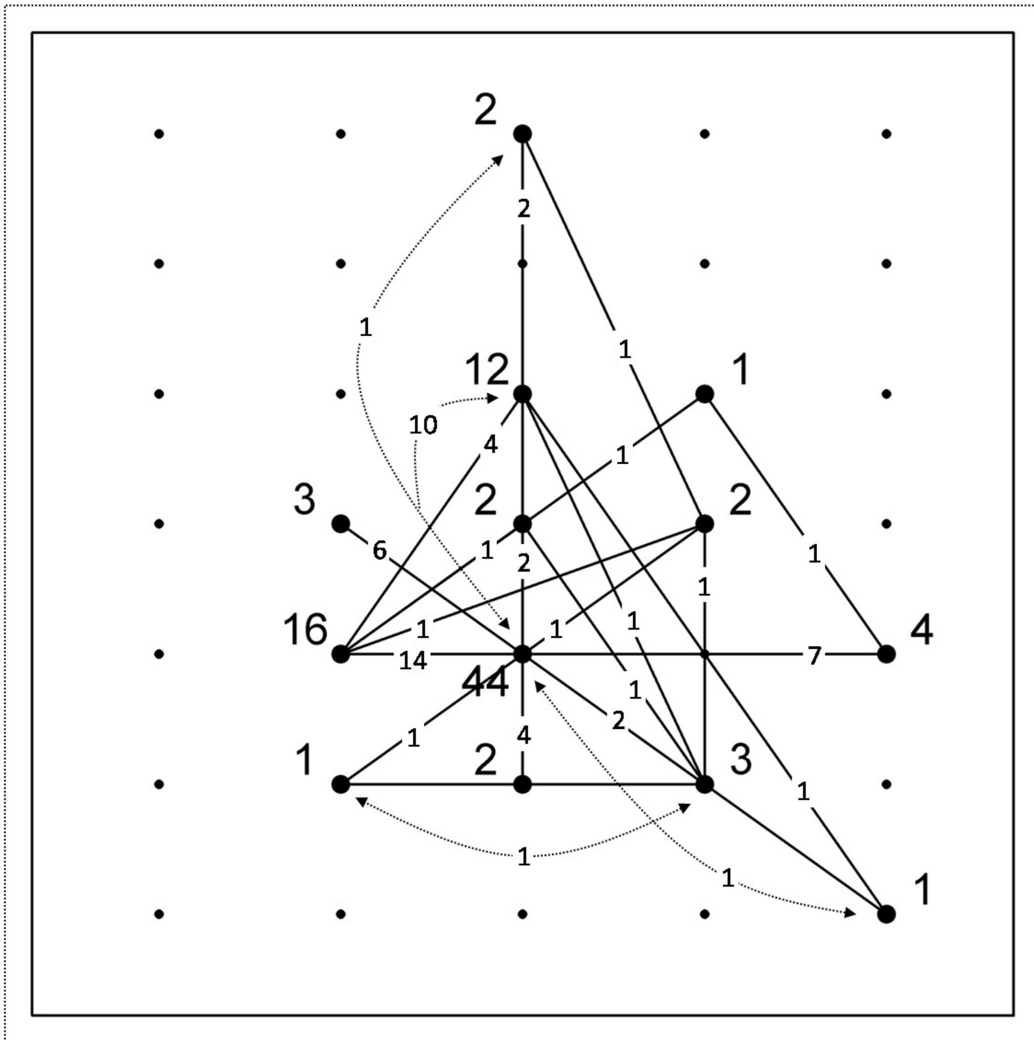

Figure 6.