IBIS
BOU international journal of avian science
Ibis (2025), **167**, 1053–1064 doi: 10.1111/ibi.13406

Absence of negative effect of GPS-tags on survival and breeding success in a long-lived territorial raptor

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GPS tracking has enabled significant advances in the study of animal movements such as migration and habitat use. However, GPS devices can affect the behaviour of tagged individuals, especially for flying animals such as birds, and may ultimately impair their reproduction and/or survival. While numerous studies have investigated the potential negative effects of GPS-tags on birds, few have simultaneously looked at these effects on reproduction and survival, with studies on the latter sometimes suffering from methodological flaws. This study investigated the effects of GPS-tagging on the breeding success and survival of a medium-sized raptor, Bonelli's Eagle *Aquila fasciata*. Forty-five breeding adults were equipped with backpack-mounted GPS-tags representing 1.2–3.5% of individual body mass. Using a recently developed capture–mark–recapture model that accounts for differences in detectability between types of tags (metal ring, coloured ring or GPS), our results showed no significant differences in survival or breeding success between GPS-tagged and banded individuals. Overall, we did not observe deleterious effects of GPS-tagging on Bonelli's Eagle that would warn against the use of GPS-tags in this species, or other medium-to-large raptors, given the relevant information they might provide for conservation.

Keywords: *Aquila fasciata*, backpack attachment, biotelemetry, Bonelli's Eagle, movement ecology, vital rates.

The rise of advanced biotelemetry techniques has allowed researchers to gather detailed data on the movements of a large number of animal species over the last three decades (Seegar *et al.* 1996, Cooke *et al.* 2004, Rutz & Hays 2009, Wilmers *et al.* 2015). The deployment of devices including Global Positioning Systems (GPS) has rapidly expanded, allowing unique insight into behaviour, as well as survival and breeding success (Meyburg & Fuller 2007, Sokolov 2011). Technological advances, in particular device miniaturization and lightening, solar-recharging batteries and increasing tag lifespan, combined with reduced prices, have allowed researchers to equip more individuals of a wider range of species with high-resolution biotelemetry devices (Wilmers *et al.* 2015, Kays *et al.* 2022).

However, the deployment of biotelemetry devices can have deleterious effects on animals, particularly on those that fly, such as bats and birds. Biotelemetry devices may alter animal behaviour, survival and breeding success (Calvo & Furness 1992, Barron *et al.* 2010, Bodey *et al.* 2018). On birds, effects have been reported such as deterioration of locomotory ability (Grey Partridge *Perdix perdix*; Putaala *et al.* 1997), direct physical injury (Red Kite *Milvus milvus*; Peniche

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et al. 2011), increased energy expenditure (Great Cormorant *Phalacrocorax carbo*; Vandenabeele *et al.* 2015), delay of migration (Northern Pintail *Anas acuta*; Hupp *et al.* 2015), and alterations in foraging (Barrow's Goldeneye *Bucephala islandica*; Robert *et al.* 2006), social behaviour (Bald Ibis *Geronticus eremita*; Puehringer-Sturmayr *et al.* 2020), preening (Gyrfalcon *Falco rusticolus*; Booms *et al.* 2011) or breeding behaviour (Rhinoceros Auklet *Cerorhinca monocerata*; Sun *et al.* 2020). Such altered behaviour can ultimately lead to reduced breeding success and survival (Bodey *et al.* 2018).

The effects of tagging with a biotelemetry device may result in both short-term and long-term effects on birds (Withey *et al.* 2001, Gillies *et al.* 2020). For example, the first months following the deployment of a biotelemetry device on an individual may have a more deleterious impact than in the following years as a consequence of stress caused by capture (Weimerskirch *et al.* 2002, Wilson & McMahon 2006). Individuals may also respond to the presence of a biotelemetry device, for example through adaptive mass loss (Croll *et al.* 1991, Evans *et al.* 2020). This raises both scientific issues (data reliability) and ethical issues, particularly when the focal species is of conservation concern. To avoid these potential drawbacks, Kenward (2001) proposed that devices should not weigh more than 3% of an individual's mass. This threshold was based primarily on disparate observations of various deleterious effects of external devices and is currently widely debated (Vandenabeele *et al.* 2011a, Tomotani *et al.* 2019, Sun *et al.* 2020). It is likely that the deleterious effects of tagging can never be completely avoided (Kenward 2001), even if species may vary considerably in their responses to device shape, weight, attachment method and deployment duration (Vandenabeele *et al.* 2011b). Thus, the impact of biotelemetry devices on the survival and breeding success of individuals must be evaluated as precisely as possible, not only for ethical concerns, but also to ensure that movement and demographic data inferred from tracking devices indeed reflect unaltered behaviours (Lameris *et al.* 2018). Answering these questions may be even more important for species whose populations are already fragile, such as raptors (Shaw *et al.* 2024).

Numerous studies have examined the potential negative effects of biotelemetry devices on birds, yet few have simultaneously looked at these effects on reproduction and survival. Many studies actually suffer from methodological flaws that could bias the effect of biotelemetry devices on survival, by not accounting for the difference in detectability between biotelemetry devices and ringed individuals, or by using return rates to a breeding or wintering site as a proxy for survival. Yet as biotelemetry data can be crucial in informing conservation (Schaub *et al.* 2024), there is an urgent need to assess the impact of biotelemetry device deployment on individual survival and breeding success (Sergio *et al.* 2015), particularly for species whose populations are already fragile.

This study investigated this question on Bonelli's Eagle *Aquila fasciata*, a long-lived territorial raptor whose French population neared extinction following a steady decline over decades, leading to only 22 pairs remaining in the 2000s (Chevallier *et al.* 2015). Since 1990, this population has been the subject of successive national action plans (Burger *et al.* 2013), allowing the population size to double over the last 20 years. The action plans have included an intensive monitoring programme, including ringing with coloured bands and GPS tracking of individuals together with an exhaustive breeding survey. Between 2009 and 2020, 45 adults were equipped with backpack-mounted GPS-tags with a Teflon harness, representing 1.2–3.5% of an individual's body mass. The Garcelon method, the harnessing method used to deploy the GPS-tags on Bonelli's Eagles, does not cause any marks, injuries, or feather or skin abrasion (García *et al.* 2021). However, it has been shown on other long-lived bird species that backpack-mounted GPS-tags could negatively affect behaviour, survival and fitness (Garrettson & Rohwer 1998, Hupp *et al.* 2015, Sergio *et al.* 2015, Thaxter *et al.* 2016). Lameris *et al.* (2018) found that geese with backpack-mounted GPS-tags had lower survival than unequipped individuals; Lopez *et al.* (2024) observed that tagged Great Black-backed Gulls *Larus marinus* had lower hatching success. Backpack-mounting has also been found to reduce survival of small-sized raptors such as the Spotted Owl *Strix occidentalis* (Paton *et al.* 1991) and Prairie Falcons *Falco mexicanus* (Steenhof *et al.* 2006), and cause physical discomfort, irritation under the wings and increased preening behaviour (Booms *et al.* 2011, Stahlecker *et al.* 2015). As the French Bonelli's Eagle population is of limited size (47 pairs in 2023), investigating whether GPS-tags indeed lower survival and/or breeding success is of critical interest for this species,

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and may also provide valuable information for GPS tracking of other medium- to large-sized raptors.

In this study, we jointly investigated the potential effect of GPS-tags on annual survival and breeding success by comparing these between equipped and non-equipped individuals. We used a recently developed capture–mark–recapture model (hereafter, CMR model: Pradel *et al.* 2022) that accounts for differences in detectability between individuals, considering the different types of tags used to monitor the individuals over time (metal ring, coloured ring or GPS-tag), as well as their dynamics (loss of ring or GPS-tag failure). Each tag type resulted in a specific detection probability; by accounting for this, we derived an unbiased survival estimate. We also assessed the effect of GPS-tag equipment on individual breeding success and on the individual's breeding partner, controlling for the age of the individual, recruitment status, the recruitment of its partner, and the weight of the tag compared to individual body mass. We conducted this analysis on females and males separately. We tested for a possible immediate (as opposed to long-lasting) effect of tagging, as a consequence of capture- and handling-related stress, and specifically investigated whether the first reproductive output immediately following tag deployment was more affected than subsequent breeding attempts.

MATERIALS AND METHODS

Model species

Bonelli's Eagle is a medium-sized monogamous long-lived raptor that reaches the northern limit of its distribution in France. Its territory there is located around the Mediterranean Sea, where the species mainly occupies scrubland around limestone cliffs used for nesting (Hernández-Matías *et al.* 2013). Highly territorial, adults are sedentary with high site fidelity over the years (Hernández-Matías *et al.* 2015). Bonelli's Eagle is considered a generalist predator with a flexible diet according to environment and prey occurrence and abundance (mainly birds and mammals, but also reptiles) (Ontiveros *et al.* 2005, Resano-Mayor *et al.* 2014). This raptor commonly hunts from a still position on a perch, snatching prey as they take off; it can also swoop on prey from soaring flight, and is often seen hunting in pairs (Ferguson-Lees & Christie 2001).

Monitoring data

Since 1990, an intensive survey of Bonelli's Eagle breeding sites in France has been carried out each year in order to identify territorial birds and to assess age at recruitment, leading to a resighting probability of approximately 80% annually for territorial individuals (Lieury *et al.* 2016). At least three visits are made each year (but generally one per week) from the mating to fledging period (February–June) (Burger *et al.* 2013) on all known breeding sites, recording the number of fledglings produced (from 0 to 2) (hereafter referred to as breeding success). Since the beginning of the mark–recapture programme, 97% of chicks born in the population have been ringed in the nest before fledging with a conventional metal ring and a coloured ring ($N = 856$ over 31 years). As metal rings are difficult to read at long distance, individuals are mostly identified by the coloured ring. Before 2015, individuals were marked with both Darvic (plastic not riveted, denoted coloured ring) and metal rings (museum, without clasp before 2009 and with clasp after 2009). However, the loss of both metal and plastic rings has been documented (Chevallier *et al.* 2015). Ring loss is estimated on sight or during capture. If not accounted for in modelling, ring loss leads to underestimated survival rates, so it is important for models to consider this (Cowen & Schwarz 2006, Arnason & Mills 2011, Touzalin *et al.* 2023). Since 2015, riveted coloured metal rings (coloured ring), which are more durable, have been used instead of Darvic rings. When individuals with a Darvic ring are captured or recaptured (to deploy GPS-tag equipment), this is replaced with a coloured metal ring. These possible changes in marking also need to be considered in modelling, as they can modify the detectability of individuals (particularly if the GPS-tag stops functioning) and in turn affect the survival estimate.

GPS-tag deployment

Between 2009 and 2020, 45 adult individuals (23 females, 22 males) from 32 different breeding sites were captured and equipped with solar-powered GPS-tags from different manufacturers (see Appendix S1). Individuals were captured using bait and a remotely activated folding net. The trap was only activated once the targeted individual was inside the capture area. A hood was then

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placed over the bird's eyes to reduce stress, and the talons were bandaged to prevent injuries. Capture usually took place outside the breeding season, in autumn or early winter. If the capture session failed during this period, further attempts were sometimes made in late spring, before the chicks fledged (23% of captures occurred during the breeding season). No breeding failures were actually recorded (ascertained by bird tracking). Tags were fitted with a backpack harness, following the Garcelon method (García *et al.* 2021). We used a non-abrasive 11–13-mm-wide Teflon harness with a central breaking point under the breast (see Appendix S2), to allow the harness to fall off after a few years (typically after 4–5 years) or to detach itself if the bird became snagged (Kenward 2001). The transmitters weighed between 20 and 48 g depending on the model: the total mass (including the Teflon harness) represented 1.83% ± 0.65 [1.23–3.51] of a bird's body mass (2.38 kg ± 4.26 [1.70–3.25]) (see Appendix S1). The bird was handled for a total of about 20 min. We did not have any cases with the two partners of a pair equipped (or even tracked) with GPS-tags simultaneously.

Analysis

Effect of GPS-tag equipment on survival

Over the period 2006–2020, the capture history of 119 territorial adults (58 females, 61 males) was recorded. An Eagle may be equipped with three types of devices, each with different detection probability (see Appendix S2): a metal ring [museum, two types have been used over time: without clasp (T1) and with clasp (T2) since 2009], a coloured ring [two types have been used over time: Darvic (T1) before 2015 and riveted coloured metal ring (T2) since 2015] and/or a GPS-tag (may be active or inactive). Photographs of the different tags used are shown in Appendix S2. Detectability varies between individuals and also over time due to tags being lost or added after physical capture.

We used a CMR model describing the evolution of an individual's state over time (Fig. 1),

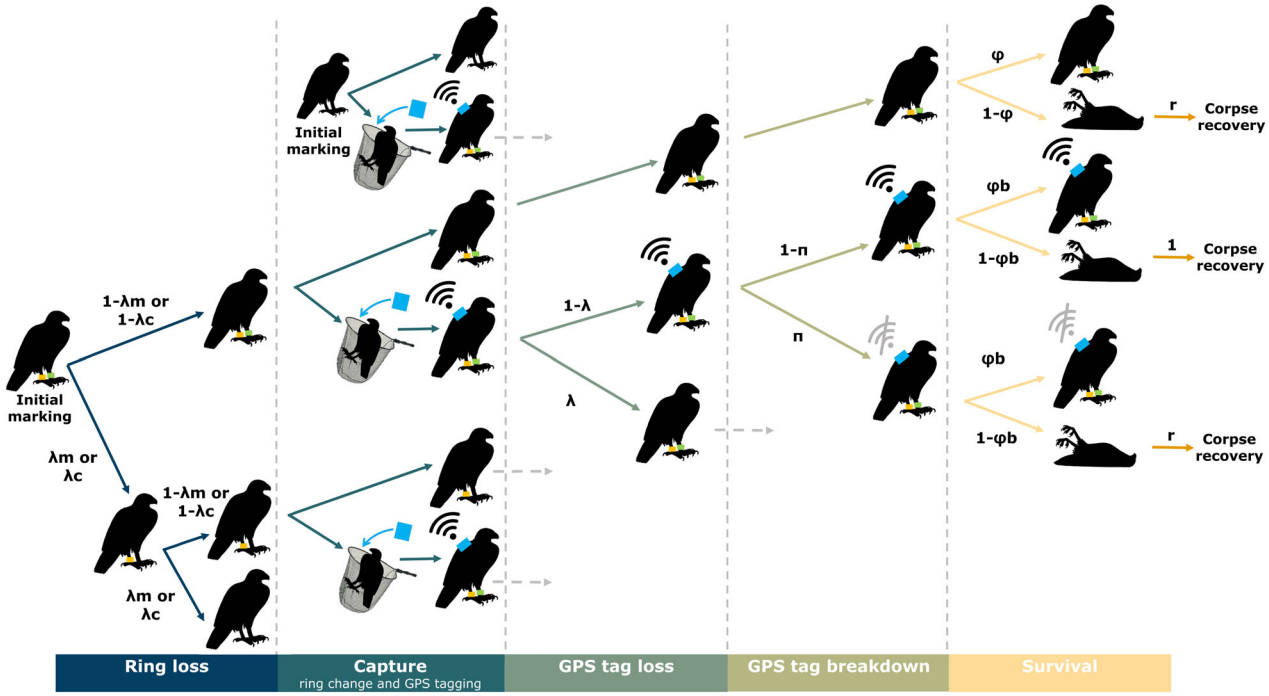


Figure 1. Representation of the states used in the model for estimating territorial adult Bonelli's Eagle survival with and without a GPS-tag. Each individual had a probability λm or λc to lose its metal or coloured ring. Each individual could be captured to be equipped with a GPS-tag. The GPS-tag could be lost with a probability λ and, if kept, fail with a probability π. Each individual could survive with a probability φ_b for individuals equipped with a GPS-tag, or φ for individuals with a band only. A corpse with or without an active GPS-tag had a recovery probability of respectively 1 or *r*. The yellow or green bands on the Eagle figure represent a metal ring or a coloured ring. The blue square represents a GPS-tag, transmitting (in black) or not (in grey) after a breakdown.

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accounting for the different types of devices used (type of GPS-tag, coloured ring and metal ring) and their role on the detection probability of individuals. The model used four transition matrixes (survival, GPS-tag state, metal ring state and coloured ring state), and estimated the parameters through the combination of these matrixes. Additionally, it distinguished the state before and after an encounter because the equipment could be changed by the observer when the individual was physically captured. The state of an individual could be (1) alive, (2) recently dead (corpse) or (3) long dead (> 1 year). A dead individual could be a corpse for 1 year, before being automatically considered long dead; a corpse might be retrieved, unlike a long dead individual. The transitions between states were governed by survival, with a distinction between φ (the survival of individuals without a GPS-tag) and φ_b (the survival of individuals equipped with a GPS-tag). The possible states for the GPS-tag were active, inactive or absent. Transitions between GPS-tag states were governed by loss and breakdown processes, with λ the probability of loss and π the conditional probability of breakdown for a retained tag. The possible states for metal and coloured rings were similar: either metal T1, metal T2 or absent, and coloured T1, coloured T2 or absent. Transitions between ring status were governed by loss processes, with type-specific rate of loss λm_1 (for metal ring)/λc_1 (for coloured ring) and λm_2/λc_2. As we did not observe any loss of T2 rings, either metal or coloured, in the data, λm_2/λc_2 values were fixed to 0. Occasionally, a T1 ring was replaced with a T2 ring on capture. When a tag was modified during a capture session, the situation before and after recapture was recorded separately. The parameters of interest were the annual survival rate with and without a GPS-tag; it was assumed that the other devices had a negligible impact. Additionally, the model provided estimates for four detection parameters: detection of a bird with an inactive (non-functioning) GPS-tag attached (pBHS), reading of a coloured ring (pc), reading of a metal ring (pm) and the recovery of a corpse without active GPS (r). The detection probability for an individual equipped with an active GPS-tag was considered certain, whether alive ($p = 1$) or recently dead ($r = 1$).

In order to consider a possible sex-specific effect of GPS-tag equipment on survival, we also designed a model that simultaneously analysed two sets of capture histories in the same model: one for males and one for females. The combined model consisted of two identical submodels, one for each sex, with sex-specific estimates of survival (φ_M and φ_{bM} for males, φ_F and φ_{bF} for females), while all the other parameters were shared between the two submodels in order to increase statistical power.

The models were implemented in Nimble v.0.11.1 (de Valpine *et al.* 2017). We specified a burn-in of 20 000 iterations that were thinned by a factor 5, and ran two chains with different initial values. Inference was obtained by 50 000 iterations. Markov chain convergence was assessed using the Gelman–Rubin statistic (R) and visual inspection of the chain-mixing. Convergence of the Markov chains was satisfactory for all parameters ($R < 1.03$). Estimates from the models on survival are presented with the mean value of the posterior distribution and the 95% credibility intervals. Posterior distributions are shown in Appendix S3.

Effect of GPS-tag equipment on breeding success

We modelled the breeding success (zero, one or two fledgling chicks) of all known breeding territories (41 sites) between 2006 and 2020. To test whether breeding success differed between GPS-tagged individuals and unequipped individuals, we fitted sex-specific linear mixed models (LMMs). As the number of fledging chicks in our dataset did not exceed two, and following the recommendation of McDonald and White (2010) that compared regression model for small counts with low variance (typical of productivity data), we considered an LMM with a Gaussian distribution rather than a Poisson distribution—the latter typically producing an expected number of fledglings greater than two (up to five), based on an observed average of 1.04 (see Results). To avoid interdependence of breeding attempts when the identity of both males and females of the pairs was known, we split the dataset by sex and implemented sex-specific models. The female dataset included 56 individuals and 246 breeding attempts. The male dataset included 51 individuals and 254 breeding attempts. The identity of the breeding individuals, as well as the year of the breeding event, were included in the model as random effects. Several fixed effects were included in the model: GPS-tag (a discrete variable with three modalities—individual without GPS-tag, individual

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with GPS-tag for the first year, individual with GPS-tag for > 1 year—in order to test for a higher impact of the equipment during the first breeding event following its deployment); GPS-tag on the partner (a discrete variable with three modalities: partner without GPS-tag; partner with GPS-tag for the first year, partner with GPS-tag for > 1 year); age (a discrete variable with two modalities: young if the individual was 4 years old or younger, old if the individual was > 4 years old; age of 4 years old was considered as the average age of sexual maturity in Bonelli's Eagle; Penteriani *et al.* 2003); percentage of the weight of the GPS-tag relative to individual body mass (a continuous variable); individual recruitment (a discrete variable with two modalities: just recruited on the breeding site; has bred for ≥ 2 years on the site); and partner recruitment (same modalities). The number of observations for the discrete variables for each model is shown in Appendix S4. All fixed effects were considered as additive except individual age and recruitment, considered herein in interaction. All models were fitted in R (R Core Team 2024) with the library glmmTMB (Brooks *et al.* 2017). Estimates from the models on breeding success are presented with their 95% confidence intervals.

RESULTS

Effect of GPS-tag equipment on survival

We did not detect any significant effect of GPS-tags on Bonelli's Eagle survival. The annual survival rate for individuals equipped with a GPS-tag, active or inactive, did not differ from the survival of individuals without a GPS-tag, as credibility intervals were largely overlapping (0.90 [0.84, 0.94] for individuals equipped with a GPS-tag compared to 0.91 [0.87, 0.94] for individuals without a GPS-tag; Fig. 2). For the model accounting for sex, we obtained similar estimates of annual survival rates between males and females for individuals with bands only (0.92 [0.87, 0.96] for females, 0.89 [0.83, 0.93] for males). The median estimate for the survival rate of females equipped with a GPS-tag (0.83 [0.74, 0.91]) was smaller than that for females banded only, while the median estimate for the survival rate of males equipped with GPS-tags (0.95 [0.88, 0.98]) was higher than that for males banded only. However, these differences were not significant, with all survival estimates showing widely overlapping credibility intervals (Fig. 3). Those small differences probably arose from a non-random selection of individuals for tagging (see Discussion). The

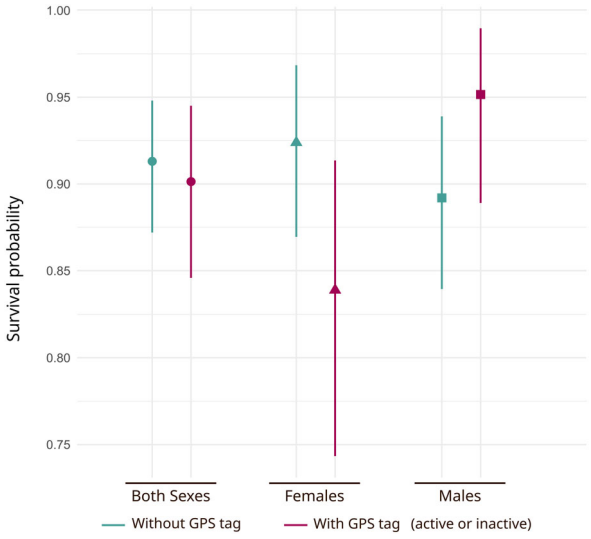


Figure 2. Estimation of Bonelli's Eagle annual survival rates and 95% credibility intervals for individuals equipped with GPS-tags (in purple) and individuals without GPS-tags (in blue). The results are represented for the model with both sexes combined (circle) and for the model with survival estimated separately for females (triangle) and for males (square).

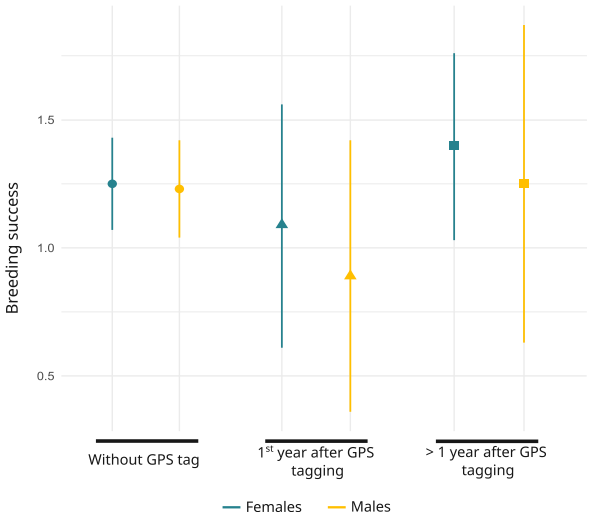


Figure 3. Estimated values and 95% confidence intervals of breeding success of Bonelli's Eagle (number of fledglings produced) for individuals not equipped with GPS-tags (circle), for individuals during their first breeding event following GPS-tag deployment (triangle) and for individuals equipped with a GPS-tag for more than a year (square). The results are presented in orange for the male model and in blue for the female model.

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Table 1. Estimation of Bonelli's Eagle survival parameters and 95% credibility intervals (CRI), with λ the probability of a lost GPS-tag, π the probability of a failed GPS-tag, λm the probability of a lost metal ring, λc the probability of a lost colour ring, pBHS the detection probability for individuals with an inactive GPS-tag, pc the detection probability for individuals with a coloured ring, pm the detection probability for individuals with a metal ring, and *r* corpse retrieval without an active GPS-tag.

	Mean	95% CRI
λ	0.18	[0.12, 0.24]
π	0.04	[0.01, 0.08]
λm	0.12	[0.07, 0.17]
λc	0.09	[0.03, 0.15]
pBHS	0.87	[0.67, 0.98]
pc	0.63	[0.54, 0.70]
pm	0.47	[0.38, 0.56]
r	0.07	[0.02, 0.18]

other parameters estimated by the survival model are shown in Table 1; those estimated by the model considering sex are shown in Appendix S3.

Effect of GPS-tag equipment on breeding success

Between 2006 and 2020, the population showed an average breeding success of 1.04 [0.97, 1.11] fledglings per breeding pair. Breeding success varied mainly according to the age of individuals (Table 2). Breeding success of individuals was 59% lower for males under 4 years old and 55% lower for females under 4 years old than for older individuals. Breeding success of newly recruited individuals was lower compared to experienced individuals: 39% lower for female recruits and 33% lower for male recruits. Regarding the impact of GPS equipment, we did not detect any significant effect of GPS-tags on breeding success for either males or females (Fig. 3), either in the first year of deployment or the following year. However, we found a non-significant trend for reduced breeding success of GPS-tagged individuals during the first breeding attempt following GPS-tag deployment, whatever the sex of the bird equipped (female: $\beta = -0.16$ [−0.6, 0.33], $P = 0.51$; male: $\beta = -0.34$ [−0.92, 0.23], $P = 0.24$).

DISCUSSION

It is difficult to precisely measure the effect of GPS-tag equipment on a population, in particular because of differences in detection between individuals with and without GPS-tags and the small number of individuals that are equipped in relation to the total population, resulting in low statistical power (Bodey *et al.* 2018). This is the first study on the impact of GPS-tags on Bonelli's Eagles to jointly assess the effect on survival and breeding success. Using a recently developed CMR model accounting for differences in detection probability between tag types, we found no effect

Table 2. Estimates, 95% confidence intervals (CI) and *P*-values of fixed effects for the sex-specific breeding success models.

	Females			Males		
	Estimate	95% CI	*P*	Estimate	95% CI	*P*
ID 1st-year tag	−0.16	[−0.66, 0.33]	> 0.05	−0.34	[−0.92, 0.23]	> 0.05
ID > 1st-year tag	0.14	[−0.25, 0.54]	> 0.05	0.01	[−0.68, 0.72]	> 0.05
Partner 1st-year tag	−0.09	[−0.52, 0.33]	> 0.05	0.20	[−0.26, 0.68]	> 0.05
Partner > 1st-year tag	−0.04	[−0.35, 0.26]	> 0.05	−0.04	[−0.41, 0.32]	> 0.05
Age - young	**−0.70**	**[−1.16, −0.25]**	**0.002**	**−0.72**	**[−1.14, −0.31]**	**0.000**
ID - recruit	**−0.49**	**[−0.81, −0.17]**	**0.002**	−0.05	[−0.68, 0.58]	> 0.05
Partner - recruit	**−0.42**	**[−0.74, −0.11]**	**0.007**	**−0.36**	**[−0.29, 0.25]**	**0.01**
% body mass	−0.05	[−0.29, 0.17]	> 0.05	−0.02	[−0.77, 0.86]	> 0.05
Age young: ID recruit	0.29	[−0.31, 0.91]	> 0.05	−0.06	[0.13, 0.46]	> 0.05

ID 1st-year tag: individuals in the first year of being equipped with a GPS-tag. ID > 1st year tag: individual equipped with a GPS-tag for more than a year. Partner 1st-year tag: partner in the first year of being equipped with a GPS-tag. Partner > 1st-year tag: partner equipped with a GPS-tag for more than a year. Age - young: age-class of individual less than 4 years old. ID - recruit: individual has recruited on a site this breeding event. Partner - recruit: partner has recruited on a site this breeding event. % body mass: percentage of the GPS-tag weight compared to the individual's mass. Age young: ID recruit: interaction effect for young individuals that have recruited. Intercept corresponds to individuals over 4 years old without a GPS-tag that have not recruited this breeding event and of which the partner has no GPS-tag and has not recruited. Significant parameters are shown in bold.

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of GPS-tags types on the survival or breeding success of Bonelli's Eagles.

Survival and breeding success of Bonelli's Eagle

The apparent survival and breeding success of territorial Bonelli's Eagles estimated here is similar to previous results on the same population (Hernández-Matías *et al.* 2011, Chevallier *et al.* 2015, Lieury *et al.* 2016) or on this species (Penteriani *et al.* 2003, Carrete *et al.* 2006). The results also highlight a strong negative effect of young age and recruitment of the individual or its partner on breeding success, as has been shown in previous studies on Bonelli's Eagle (Penteriani *et al.* 2003, Carrete *et al.* 2006, Hernández-Matías *et al.* 2011).

The CMR model that we used (Pradel *et al.* 2022) can account for differences in detectability between types of tags and consider the possibility of changes in marking over time. This allows for a more precise estimation of adult survival than in previous studies on the same population (Chevallier *et al.* 2015, Lieury *et al.* 2016). Better modelling of tag-specific detectability also avoids overestimation of the survival of GPS-tagged individuals, which has been an issue in other studies investigating the GPS-tag effect. This improvement in precision was also helped by an increased effort to annually check individual rings or information from GPS-tags, providing very precise data on the timing of death.

Effect of GPS-tags on the survival and breeding success of Bonelli's Eagle

We found no evidence to conclude an effect of GPS-tags on the survival of Bonelli's Eagle. We observed that the annual survival rate of GPS-equipped adults was not different from individuals that were banded only. When further considering sex in the analysis, the survival rate of females equipped with a GPS-tag was lower than the survival rate of females banded only. By contrast, the survival rate of males equipped with a GPS-tag was higher than the survival rate of banded males. For both sexes, however, the two survival estimates had widely overlapping credibility intervals, indicating non-significant differences. We expected that males would be more affected than females if the tag affected Eagle survival. Indeed, male Bonelli's Eagles are lighter than females and the burden imposed by the tag represents a higher proportion of bird mass, and they also move more during breeding than females (López-López *et al.* 2022, Viollat *et al.* 2024). We cannot see any biological reason why tagged males would have a higher survival compared to banded-only males and it is therefore highly likely that the observed differences were the consequences of a slight random bias in the selection of individuals for tagging (Bodey *et al.* 2018). The original objective of equipping Bonelli's Eagles with GPS-tags was to obtain data from at least one adult per nesting site in France for a minimum of 1 year to accurately assess their home-range. However, some sites show a high turnover of birds (Ravayrol *et al.* 2022). To ensure sufficient tracking duration, GPS-tags have thus been deployed on several individuals on these sites, after the death or abandonment of the site by the tracked individual. Additional GPS-tags have been deployed on sites associated with low survival rates, particularly some with high female mortality, rather than being randomly distributed throughout the population. This successive tagging of individuals on the same sites could potentially create an artificial difference in survival rates between GPS-tagged and banded individuals. We identified a site that could be particularly problematic in our study (site 20), where four females were successively equipped (see Appendix S1). To test our hypothesis of potential bias resulting from sites with high mortality, we ran our model on survival without the four individuals from site 20 (see Appendix S5). Without these four individuals, the negative effect of GPS-tags on the survival of females disappeared. The slightly negative effect of GPS-tags observed on the survival of females thus seems to come from bias in the equipping of individuals rather than a real effect of GPS-tag deployment.

Our results are in line with what has been observed in other medium-sized raptor species (e.g. Black Kite *Milvus migrans*; Sergio *et al.* 2015), for which no deleterious effects of GPS-tag deployment have been highlighted on breeding success or survival. In their meta-analysis, Bodey *et al.* (2018) noted that significant effects of GPS-tags mostly concerned species with flapping flight, but not soaring species (such as Bonelli's Eagle) and most other large terrestrial birds (Duriez *et al.* 2014). Soaring involves lower energy

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costs (Pennycuick 2008), which may mitigate the impact of tagging. Aside from species with flapping flight, tagging also has been found to have a negative association with survival and breeding in species with long migration distances (Bodey *et al.* 2018): this also involves a high energy cost for individuals (Alerstam *et al.* 2003, Klaassen *et al.* 2014). It thus seems reasonable to expect that sedentary species, such as Bonelli's Eagle, will be less affected by tagging than migratory species.

Regarding the impact of GPS-tags on the breeding success of Bonelli's Eagles, no significant effect was observed on the individual or its partner. Although there was a slight decrease in breeding success for GPS-tagged individuals during their first breeding attempt following being equipped, this was not statistically significant for either sex. However, the impact of GPS-tags on breeding success during an individual's first breeding attempt after GPS deployment may not be entirely negligible. Indeed, females experienced a 13% decrease in breeding success, while males experienced a 27% decrease compared to individuals without GPS-tags, despite the overlapping confidence interval. Yet the impact of GPS-tag deployment on the first breeding event was much smaller than the impact of recruitment or age, and this trend disappeared in subsequent years. This could be explained by the bird's habituation to the equipment (Gillies *et al.* 2020) or by a carryover effect resulting from the stress experienced during capture (Weimerskirch *et al.* 2002, Wilson & McMahon 2006).

The ratio between the weight of GPS-tags and body mass is a well-studied and controlled parameter to minimize the potential impact of GPS-tags on individuals (Wilson & McMahon 2006, Casper 2009, Vandenabeele *et al.* 2011a). As females are generally larger than males (Ferguson-Lees & Christie 2001), we expected that the weight of the tag would have a greater impact on the breeding success of males. Yet no significant effect of tag weight was found on the breeding success of males or females, even though eight individuals (17%) had tags that exceeded 3% body mass, the threshold most commonly used (Bodey *et al.* 2018). It is possible that the lack of significance is a consequence of the low number of individuals with heavy tags compared to body mass. Therefore, the 3% threshold value for birds, as proposed by Kenward (2001), is not applicable for all species. Indeed, it has been debated in numerous studies (Barron *et al.* 2010, Vandenabeele *et al.* 2011a, Bodey *et al.* 2018, Tomotani *et al.* 2019, Sun *et al.* 2020). As our study subject is a medium-sized raptor, we have the option of using tags with a relatively low weight compared to the bird's mass. This may not be possible in smaller birds of prey with current technology (Bodey *et al.* 2018).

CONCLUSIONS

In this study on a long-lived territorial species, our results show no deleterious effects of GPS-tag deployment that could affect its dynamics or would caution against the use of GPS-tags on this or similar species, given the important information these tags provide for conservation purposes. The use of GPS-tags on Bonelli's Eagles is a very valuable tool: for example, to define home-ranges in order to limit the development of infrastructure within these, or to better understand habitat use in order to better manage habitat to improve the conservation of this species. To further our knowledge, it would be valuable to test the effect of equipping individuals with GPS-tags on species with different flight strategies (the Bonelli's Eagle mainly glides) and on juvenile stages. As juveniles are still growing and spend more energy during the dispersal process (Bonte *et al.* 2012), it is possible that the effect of GPS-tags on juveniles may be stronger and require further investigation. Furthermore, even if we do not highlight here any effect of GPS-tagging on demographic parameters of Bonelli's Eagle (breeding success or survival), GPS-tagging could still alter behaviours such as individual movement patterns.

The Bonelli's Eagle ringing programme in France is ethically approved by the Research Centre on the Biology of Bird Populations (CRBPO). We are grateful to the local network of volunteers and collaborators who have been monitoring the Bonelli's Eagle population since 1990 and all those who took part in the captures and telemetric monitoring. We also thank the Métropole Aix-Marseille-Provence, Parc national des Calanques, Métropole Toulon-Provence-Méditerranée, DDTM 13, 83, 34, 66,11,30; DREAL PACA, DREAL Occitanie, Syndicat de gestion des Gorges de l'Ardèche, Parc naturel régional des Alpilles, Parc naturel régional de la Sainte-Baume, Parc naturel régional du Haut Languedoc, CEN Occitanie, Groupe ornithologique du Roussillon, LPO Aude, LPO Hérault, LPO Auvergne Rhône Alpes, Parc naturel régional de la Narbonnaise, European Commission, Centre ornithologique du Gard, Grand Site Sainte-

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Victoire, Syndicat mixte de gestion du Salagou, Communauté de communes du Grand Pic Saint-Loup, Communauté de communes Vallée de l'Hérault, Syndicat mixte des Gorges du Gardon, Victor Garcia Matarranz, Ministerio de Agricultura, Alimentación y Medio Ambiente and Fondation d'entreprise Barjane. We also thank the reviewers for their constructive and insightful comments.

AUTHOR CONTRIBUTIONS

Lise Viollat: Writing – original draft; writing – review and editing; conceptualization; methodology; investigation. **Roger Pradel:** Conceptualization; methodology; writing – original draft; validation. **Cécile Ponchon:** Investigation; supervision; writing – original draft. **Alain Ravayrol:** Investigation; supervision; writing – original draft. **Alexandre Millon:** Conceptualization; methodology; writing – original draft; validation; writing – review and editing; investigation. **Aurélien Besnard:** Conceptualization; methodology; investigation; validation; writing – original draft; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

FUNDING

None.

ETHICAL NOTE

None.

Data Availability Statement

The codes and data that support the findings of this study are available on Zenodo at https://doi.org/10.5281/zenodo.14811189.

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Received 22 October 2024;
Revision 5 February 2025;
revision accepted 2 March 2025.
Associate Editor: Kurt Burnham.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Individual characteristics and GPS-tag deployment.

Appendix S2. Device equipment on Bonelli's Eagles.

Appendix S3. Survival model estimations.

Appendix S4. Breeding success models.

Appendix S5. Results of survival models excluding individuals from site with known high mortality.

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