Animal Biotelemetry

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Can waterfowl buffer the mortality risk induced by GPS tags? A cautionary tale for applied inference across species

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Abstract

GPS tags have become a common tool in ecological studies of animal behaviour and demography despite previous research indicating negative impacts on vital rates across a variety of taxa. Many researchers face tradeoffs when deciding whether they are an appropriate tool because GPS tags may impact vital rates, but they provide detailed data on movements and behaviour that often cannot be obtained in other ways. Using band recovery data, we evaluated the strength of effects induced by GPS tags on annual mortality of adult females across 13 waterfowl taxa, and examined whether taxa with a slower life-history strategy and larger body size were more resilient to GPS tag effects than their fast-lived counterparts with small body size. All species were exposed to hunting, which may interact with underlying processes affecting the impact of GPS tags on mortality, but also allowed for robust analysis of overall annual mortality. Hazard ratios, indicating the risk of death for individuals wearing GPS tags compared to those wearing only metal bands, ranged from 1.13 to 3.25 and the mean proportional difference in survival between marker types across species was 0.33. The magnitude of tag effects was surprisingly consistent across life-history tempo and body size, indicating that slower-lived species did not buffer the effect of wearing GPS tags. Our results highlight that even large, long-lived species, which are generally better at buffering their mortality against environmental adversity, are not immune to the effects GPS tags can have on survival and mortality. The results of our study emphasize the importance of testing for such effects across taxa in future research as technology advances.

Keywords Bio-logger, Demographic buffering, GPS tags, Marker effects, Survival, Transmitters, Waterfowl

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Introduction

Bio-logging devices such as global positioning system (GPS) tags have become ubiquitous in ecological studies of animal behaviour, movement, and demography and have largely replaced very high frequency (VHF) radio tags across many taxa. Various models of GPS tags can send location, acceleration, and other data points remotely through satellites or mobile phone networks, thus greatly reducing personnel time and effort that would have traditionally been spent tracking and triangulating telemetered individuals [37, 82]. GPS tags can also provide data at much finer spatial and temporal resolutions than VHF radio tags. When deploying GPS tags (hereafter tags) for the purpose of studying behaviour or demography, such markers must not affect the parameters of interest. When this assumption is violated, marked animals are not representative of the larger unmarked population, resulting in biased estimates of focal parameters and, in some cases, affecting the inference that can be made from tagged individuals [52]. While empirical tests have been conducted on the effect of tag weight on survival, reproduction, and activity of some birds [30, 54, 59, 70], data have been lacking on many groups of birds, especially pertaining to the magnitude of tag effects. Unlike collars used for mammals, GPS tags are typically attached to the back of birds via harnesses of varying materials and attachment styles [55], around the individual's legs resting on their rump [77], or occasionally as neck collars on larger-bodied birds like geese and swans [42]. Tag impacts on the biology of any species of interest must continue to be evaluated and transparently reported because technology continually advances and environmental conditions change [51]. Additionally, researchers should continue to test the assumption that markers do not impact an animal's ability to survive, especially if environmental conditions change over time [51] or if the technology and attachment styles change, so that information attained from tagging studies effectively guides conservation actions.

Multiple studies over the past several decades have evaluated the effects tags can have on the birds they adorn. While results have been mixed with respect to study duration and the specific behaviours or vital rates of interest, researchers have observed negative impacts on everything from migration return rates [46],odds ratio of tagged birds returning compared to control group = 0.32) to body mass among harvested gamebirds associated with tag attachment [22],tagged birds weighed 133 g less than unmarked females, SE = 25 g [13–20% of average body mass]). Bodey et al. [10] provide a comprehensive review of the effects of bio-logging devices on birds in which they found significant negative effects of harness and tail-mount tags on survival across taxa. Geen et al. [25] found that the reporting of tag effects on birds declined over time and increased with device mass, indicating that with increased ubiquity of devices comes the possible acceptance of devices by the ecological community despite possible biases that may remain unreported [47]. In terms of effects on survival and mortality, no studies to date have directly compared species' abilities to cope with tag effects across life-history strategies, but there is some evidence that larger species with slow life-history strategies might not experience the same magnitude of tag effects as faster-lived counterparts. For example, Constantini and Moller [19] and Brlik et al. [11] both found stronger negative effects of geolocators on smaller bird species and those with shorter migration distances (i.e. fast-lived), with survival effect sizes (Hedges' g) ranging from − 0.2 to − 0.1. In contrast, slow-lived Trindade petrels (*Pterodroma arminjoniana*) attached with similar geolocator devices exhibited no difference in apparent survival compared to untagged counterparts [61]. Still, larger and more long-lived species can nonetheless be affected by tags. For example, Manx shearwaters (*Puffinus puffinus*) were found to considerably alter their foraging behaviour during the breeding season to maintain the same level of breeding success as their unmarked counterparts [29]. The arena of avian bio-logging is thus perfectly primed for an evaluation of tag effect size across the life-history spectrum.

Among birds, waterfowl are particularly relevant for comparing tag effects across a range of body sizes and life-history strategies. Most of their populations are exposed to harvest and thousands of individuals are outfitted with leg bands (i.e. metal rings) annually, often providing a large sample size of recovered birds. These robust sample sizes allow for the assessment of device impacts on survival using traditional band-recovery methods by comparing recoveries between birds marked with both rings and GPS tags and birds marked only with rings. Though waterfowl are relatively large-bodied birds that one might a priori believe to be resistant to tag effects, Lameris and Kleyheeg [47] observed major negative impacts in 17% of waterfowl studies (and 40% of studies reporting potential effects) where tag effects were reported, and called for greater reporting of effects among researchers. Additionally, waterfowl cover a large range of life-history strategies and body sizes, from short-lived, small cinnamon teal (*Spatula cyanoptera*) that attempt to reproduce during their first breeding season after hatching, to black brant (*Branta bernicla nigricans*) that have high adult survival, delayed age at first reproduction, and skip reproduction attempts thereafter if internal states or environmental conditions are unfavourable [43]. We can therefore test whether effect sizes of GPS tags on mortality vary across life-history strategies and whether slow-lived or large-bodied species can buffer the effects.

Though any effects of tags should be of concern, species should not be expected to exhibit uniform responses (i.e. effect sizes) to wearing GPS tags because they vary widely in their body size and life-history strategies. Larger-bodied species may experience less drag during flight when fit with tags on their backs compared to smaller species, and might be better equipped to carry comparably sized tags as a result of their larger size [64]. Additionally, fitness of long-lived species with slow life histories is highly sensitive to proportional changes in adult survival, whereas fast-lived species are typically more sensitive to proportional changes in reproductive rates [33, 69]. The demographic buffering hypothesis predicts that species should possess traits that allow them to buffer the vital rates having the greatest impact on fitness against environmental adversity (Fig. 1), [24, 28, 65]. If they did not, such changes would have the most deleterious impacts on fitness in time-varying environments. Outfitting an individual with a tag presents a potential alteration of their experience, and therefore we might predict a lower impact of tags on adult survival in species with slow life histories because they have the opportunity to plastically adjust activities to maintain their chances of surviving (e.g., skipped breeding, higher vigilance rates, etc. [7]). We might also expect greater effects of GPS tags on adult survival and mortality in fast-lived species because of their greater investment in reproduction at the cost of allowing survival to be more greatly affected by external factors (e.g., impacts imposed by tags,see Fig. 1). If tag effects exist and magnitudes are similar across the spectrum of body size and life-history strategy, we might conclude that effects on larger or slower-lived species are so great that the effect of wearing GPS tags overrides their evolved ability to plastically invest in longevity (Fig. 1). Such effects would be of concern in studies using GPS-marked individuals to inform demography. Changes in annual survival and mortality attributed to GPS tags might also act as an indicator of sub-lethal marker effects on traits associated with survival, which would warrant further investigation into plausible effects until technological advances eliminate them altogether.

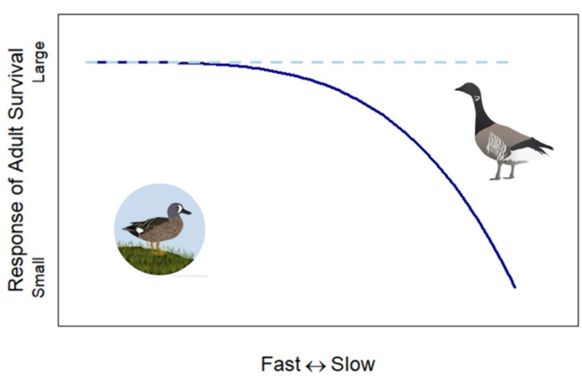

Fig. 1 Conceptual schematic illustrating the demographic buffering hypothesis (solid line), inspired by Morris and Doak [57] and Morris et al. [58]. The response of adult survival to environmental fluctuations or adversity is adaptively reduced (small response) in long-lived species with slow life histories because larger responses would most negatively affect fitness in species with these life histories [65]. Conversely, a flat relationship would indicate a lack of demographic buffering and possibly maladaptive responses of slow life histories to environmental fluctuations or adversity (dashed line)

Using waterfowl band-recovery data, we compared annual survival and mortality among 13 North American waterfowl species fitted with both GPS tags and a United States Geological Survey (USGS) metal leg band, to those affixed with only a leg band, predicting that GPS tags would (1) negatively impact annual survival (and positively impact annual mortality) across waterfowl species, with potential decreases in effect size over time, and (2) the severity of adverse effects of tagging would depend on body size and life-history tempo, and should be less pronounced in large, slow-lived species compared to fast-lived species due to the physics associated with drag or greater ability of demographic buffering in the former group (see Fig. 1). Our primary goals were to evaluate the impacts of GPS tags on annual survival and mortality across the spectrum of waterfowl life-history strategies and body size, to motivate stakeholders to consider whether they provide appropriate inference for guiding conservation decisions associated with demographic parameters, and to further encourage researchers to measure and account for their effects in future studies as technology advances.

Methods

Data organization

We downloaded banding release and recovery records from the GameBirds Database (Bird Banding Lab [BBL], USGS Patuxent Wildlife Research Center). We subset the data to species of ducks and geese that breed in North America and have been marked with GPS tags from 2006 to 2022 (recovered until the 2022–2023 hunting season), which for inclusion in our analysis were also required to have been marked with a metal leg band. We restricted data to birds released alive in the same 10-min geographical block in which they were banded and to birds banded in the United States or Canada. We also restricted our analysis to birds banded as after-hatch-year (AHY) females, given that most of our total transmitter sample comprised AHY females and most studies deploying GPS tags affix them to this age-sex class. We next restricted band-only data to the geographic flyways and years during which GPS tags had been deployed for each species to ensure the consistent geographic areas and time periods for which survival and mortality were compared between GPS-tagged and 'band-only' samples (years listed in Table 1). In other words, we started the band-only analysis in 2013 for mallards (*Anas platyrhynchos*) even though band releases date back to the 1960s because GPS tags were not deployed on mallards until 2013. We removed any record in the band-only data for which the bander included an "Additional Information" code that indicated any other type of auxiliary marker was affixed to the bird or other type of experimental manipulations (e.g., 19: Blood sample taken plus an additional auxiliary marker, 89: Transmitter—Obsolete, 85: Miscellaneous). This included nasal discs, wing tags, plastic neck collars, and any type of VHF transmitter.

We identified birds with GPS tags either by subsetting records with the Additional Information code 80 (Satellite/Cell/GPS Transmitter) or by searching through comments made on records associated with other Additional Information codes. In some cases, we searched the literature to locate studies and reports that could verify specific birds were fitted with GPS tags if comments were inconclusive in the original banding data. Given that GPS tags are an increasingly used technology, often by multiple investigators studying the same species simultaneously, we removed release data (and associated recoveries) from 2020 or later contributed by investigators involved in ongoing studies who did not wish for their data to be included ($n < 310$ AHY female releases across all species and < 40 recoveries after all other data filtering).

Different species of waterfowl are fitted with GPS tags during different seasons rather than solely during typical pre-hunting-season banding operations. For such species we split the dataset by release date to fit a seasonal band-recovery survival model rather than excluding a large portion of the tagged sample. The number of seasons of release within a given year varied from one to three for each species depending on what the data could support. For species with year-round releases, we considered birds banded from January–April as winter releases, May–July as summer releases, and August–September as part of the

Table 1 Results from the Bayesian band recovery model for 13 taxa of waterfowl fitted with only a metal band or also with a GPS tag

Species	S_{band} (SD)	S_{tag} (SD)	HR_{avg} (*f*)	Years	No. bands recovered (No. released)	No. tags recovered (No. released)
LSGO[b¥]	0.87 (0.02)	0.86 (0.10)	1.13 (0.42)	2013–2022	2876 (41,406)	6 (101)
GSGO[a]	0.80 (0.03), 0.79 (0.04)	0.41 (0.13), 0.61 (0.15)	4.29 (0.99), 2.21 (0.88)	2006–2010, 2019–2022	136 (1771), 43 (762)	19 (87), 24 (116)
GWFG[b]	0.86 (0.02)	0.75 (0.12)	1.98 (0.80)	2012–2022	967 (7157)	12 (131)
BLBR[a]	0.91 (0.02)	0.79 (0.07)	2.68 (0.96)	2006–2022	283 (14,076)	10 (122)
CANG[b]	0.76 (0.01)	0.56 (0.13)	2.26 (0.93)	2008–2022	20,467 (89,748)	27 (341)
WODU[a]	0.55 (0.02)	0.26 (0.19)	2.71 (0.91)	2019–2022	780 (8976)	5 (33)
CITE[a]	0.56 (0.03)	0.25 (0.11)	2.61 (0.99)	2017–2022	40 (1604)	15 (119)
GADW[a]	0.62 (0.03)	0.48 (0.15)	1.62 (0.82)	2015–2020	41 (434)	12 (105)
AMWI[a]	0.56 (0.04)	0.48 (0.24)	1.58 (0.62)	2019–2022	25 (676)	3 (63)
MALL[a]	0.60 (0.01)	0.48 (0.06)	1.45 (0.97)	2013–2022	10,018 (108,829)	90 (1140)
ABDU[a]	0.60 (0.02)	0.45 (0.19)	1.77 (0.78)	2007–2022	894 (14,054)	5 (116)
NOPI[a]	0.59 (0.04)	0.46 (0.22)	1.77 (0.71)	2017–2022	7 (127)	5 (95)
LESC[c]	0.56 (0.03)	0.29 (0.13)	2.34 (0.97)	2006–2022	312 (7813)	8 (111)

Hazard ratios were calculated as the ratio of the mortality hazard for individuals wearing a GPS tag and a band to the hazard for individuals wearing only a metal band. Species and sub-species included lesser snow goose (LSGO), greater snow goose (GSGO), greater white-fronted goose (GWFG), black brant (BLBR), Canada goose (CANG), wood duck (WODU), cinnamon teal (CITE), gadwall (GADW), American wigeon (AMWI), mallard (MALL), American black duck (ABDU), northern pintail (NOPI), and lesser scaup (LESC). We used time-averaged hazard rates calculated from a log-linear model that accounted for random time effects (for the band-only group) or time periods (for the band plus GPS tag group) to compute the hazard ratios and survival probabilities. All numbers are rounded to the second decimal place. SD indicates the standard deviation (i.e. sampling uncertainty) of the posterior and *f* is the proportion of the hazard ratio posterior greater than 1, where hazard ratios greater than 1 are indicative of higher mortality associated with GPS-tagged birds than band-only birds. Point estimates for species with temporal or geographic variation in the model structure were computed using averaged hazard rates

HR hazard ratio

[a] Backpack attachment style comprised majority of sample

[b] Neck collar attachment style comprised majority of sample

[c] Implant attachment style comprised majority of sample

[¥] Geographic variation in LSGO survival necessitated assigning Canadian provinces to geographic Flyways. All Flyway assignments are noted in Table S1 pre-hunting-season sample (hereafter: pre-season). Species with three seasons of release included greater white-fronted geese (GWFG; *Anser albifrons*), Canada geese (CANG; *Branta canadensis*), cinnamon teal (CITE), gadwall (GADW; *Mareca strepera*), mallard (MALL), and lesser scaup (LESC; *Aythya affinis*). For species with band releases occurring during two distinct time periods, we assigned releases from May–September as summer releases and those occurring from January–April as winter. Species with two seasons of release included lesser snow geese (LSGO; *Anser caerulescens caerulescens*), American wigeon (AMWI; *Mareca americana*), and American black ducks (ABDU; *Anas rubripes*). For yet other species, including greater snow geese (GSGO; *Anser caerulescens atlanticus*), black brant (BLBR), and wood ducks (WODU; *Aix sponsa*), we restricted releases to those solely from May–September (i.e. one season of release), whereas northern pintail (NOPI; *Anas acuta*) were restricted to releases from January–April. We restricted the band recoveries to consider only birds harvested and reported during the North American hunting seasons, which included August–January for all species except snow geese, which included August–June to allow for recoveries from the spring light goose conservation order, which allows for harvest of snow geese past the end of the traditional waterfowl hunting season into the spring (Reed and Calvert [48, 68]). We retained species in our analysis for which there were > 3 hunter recoveries of individuals outfitted with both bands and GPS tags, which included the 13 species and sub-species listed above. Though other species were frequently fitted with GPS tags, there were too few hunter recoveries (or none) of these individuals for the species to be included in our analyses. We compiled band-recovery data into m-arrays, which are compact versions of an encounter history indicating how many individuals of a cohort marked in a given year are recovered in the same or subsequent years in matrix form [14, 39].

Estimation of GPS tag effects on annual survival and mortality

We did not use any location or other data collected by GPS tags specifically, only band releases and hunter recoveries of banded and GPS-tagged birds to facilitate comparable evaluations of survival and mortality between marker categories. Using these data, we fit a Bayesian band-recovery model to estimate annual survival and mortality of AHY females for each species with and without GPS tags [12, 71, 81]. We included either one (pre-season banding operations, or for pintail, a winter banding operation, two (pre-season banding operations and winter banding operations, or three (pre-season, winter, and summer banding operations seasons depending on the data to account for differences in exposure time to mortality events. We calculated annual survival as a derived multiplication of monthly survival, which we kept constant across seasons of release because of sample size restrictions (i.e. we could not estimate differences in survival and mortality based on season of release while also attempting to estimate tag effects [20, 31],).

We fit a band-recovery model for each species separately, whereby mortality was modelled on the log-hazard scale and Seber conditional band recovery probabilities were modelled on the logit scale using $\text{link}(A) = \boldsymbol{X\beta} + \varepsilon_t$. Here, A denotes either a mortality hazard or recovery probability, $\boldsymbol{\beta}$ denotes a vector of estimated coefficients, $\boldsymbol{X}$ denotes a matrix of linear predictors, and for some A, ε_t denotes a random effect for temporal variation among years. For mortality hazards, we first evaluated effects of geographic area of release. This involved a determination of which geographic Flyways (as designated by the US Fish and Wildlife Service: Atlantic, Mississippi, Central, and Pacific; https://www.fws.gov/partner/migratory-bird-program-administrative-flyways; Table S1) had both band-only and band plus GPS tag releases for a given species, and then we modelled differences in mortality hazards across pertinent Flyways using an intercept offset evaluated relative to a reference Flyway, which was set to the Flyway with the largest number of band releases for a given species. Analyses at smaller spatial scales were not possible because of limited sample size for several species. If the proportion of the posterior > 0 or < 0 (labelled f) for each Flyway's intercept offset was < 0.15 or > 0.85, we retained the geographic variation among those Flyways, whereas if f was between 0.15 and 0.85, we removed the intercept offset for such Flyways and they were subsequently treated as equivalent to the reference Flyway [13]. Therefore, each model could include variation in mortality by all Flyways, some Flyways, or no geographic variation. To evaluate whether the effects of GPS tags on mortality may have changed over time, we separated mortality of birds with GPS tags into an early period and a late period, dividing the total number of years since GPS tags were initially deployed in half. This method allowed us to assess change in survival over time without constraining such effects to unrealistic trends [44, 79]. We did this for all species with greater than five years of GPS tag releases, which excluded American wigeon and wood ducks from the evaluations of possible change in tag effects over time. We used the same thresholds described above to evaluate whether the data supported this temporal effect for GPS-tagged birds of each taxon, simplifying to a constant mortality hazard over time if $0.15 < f < 0.85$. Final model structures are reported in Table S2. The only species for which the model structure differed from the above method was greater snow goose, which had an 8 year lapse in GPS tag releases. We therefore fit the band recovery model to the first five years of releases (2006–2010) and the latter four years of releases (2019–2022) separately to account for the lack of indirect GPS tag recoveries during the interim years. To account for temporal variation in mortality for band-only birds associated with robust sample sizes, we included a random time effect ε_t that followed a normal distribution with mean 0 and standard deviation σ_t in models for each species except those with fewer than five years of GPS tag releases (again, American wigeon and wood ducks). These models for temporal variation allowed us to account for important process-based heterogeneity in the data and assess possible convergence between mortality of band-only and GPS-tagged birds over time, presumably in response to improvements in GPS tag technology or styles of attachment (which could not be explicitly examined because attachment style was not always reported for each tagged individual). For Seber recovery probabilities, we included an intercept and an offset for direct recoveries (i.e. birds recovered during the hunting season immediately following release) specific to each season of release supported for a given species, where indirect recoveries were the reference level. Additionally, we included an offset for GPS-tagged individuals to compare their conditional band recovery probabilities to individuals wearing only a metal band.

We specified normal priors for all tag-related coefficients on the logit scale for Seber recovery probabilities that yielded vague priors on the real parameter scale [62]. We specified informative priors for the mean annual survival of band-only birds using published survival estimates and their associated metrics of uncertainty, transformed to the log-hazard scale for mortality (Tables S3-S4). We sampled posterior distributions of each parameter using a Markov chain Monte Carlo algorithm [27] in JAGS 4.3.0 [66], using the jagsUI package in Program R (R Core Team [67]). We present the final structure of each taxon-specific model supported by the data and the derived annual survival probabilities at the level of variation supported (Figs. 2, 3). We sampled the posterior distributions of the parameters using three chains that each included 50,000 MCMC iterations with a burn-in of 25,000 and thinned each chain to keep every 25th value. We examined Gelman and Rubin [26] statistics for all parameters to ensure $\widehat{R} \leq 1.1$ and visually inspected trace plots to check for posterior chain convergence [34]. We report means of posterior distributions and 90% Bayesian credible intervals where appropriate, in addition

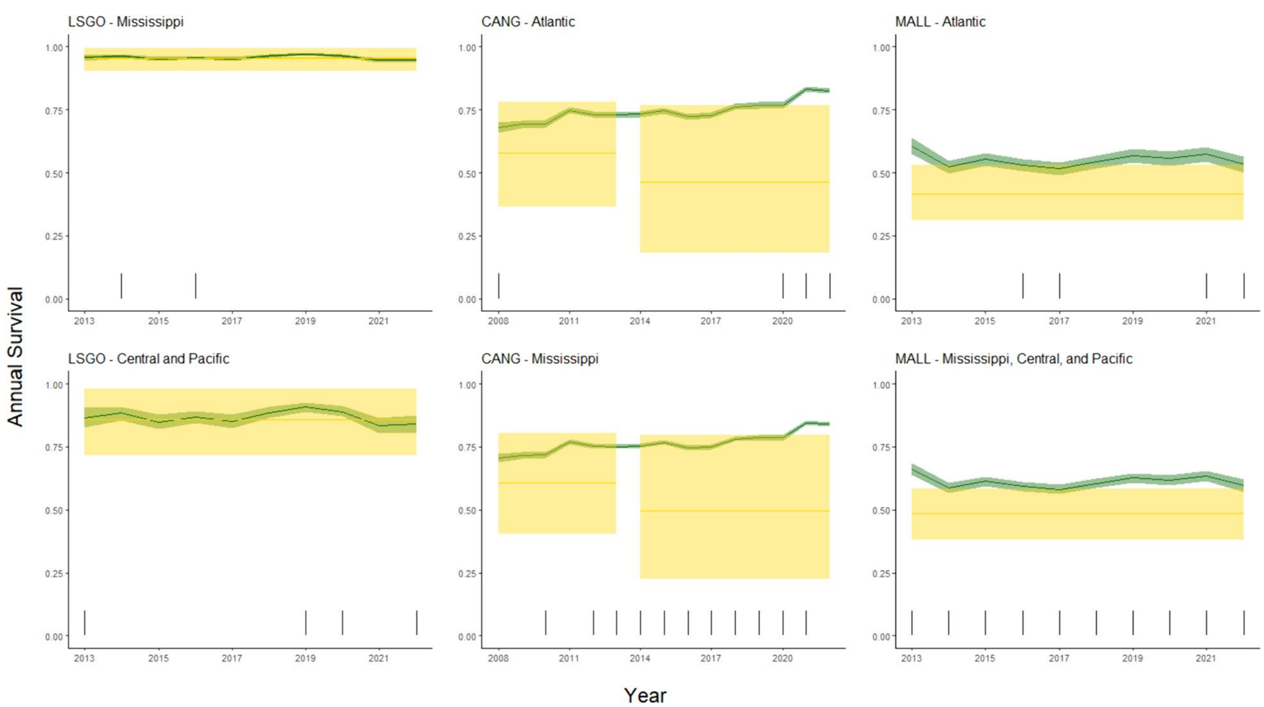

Fig. 2 Time series of adult female annual survival of the three species of waterfowl for which survival varied by flyway of release. Annual survival of birds fitted with both bands and GPS tags is represented by gold and that of birds fitted only with a metal leg band is represented by green. Each column within the panel represents a different species, with four-letter codes indicating species and sub-species as follows: LSGO = lesser snow goose, CANG = Canada goose, and MALL = mallard. Tick marks on the x-axis indicate years during which GPS tags were deployed on birds

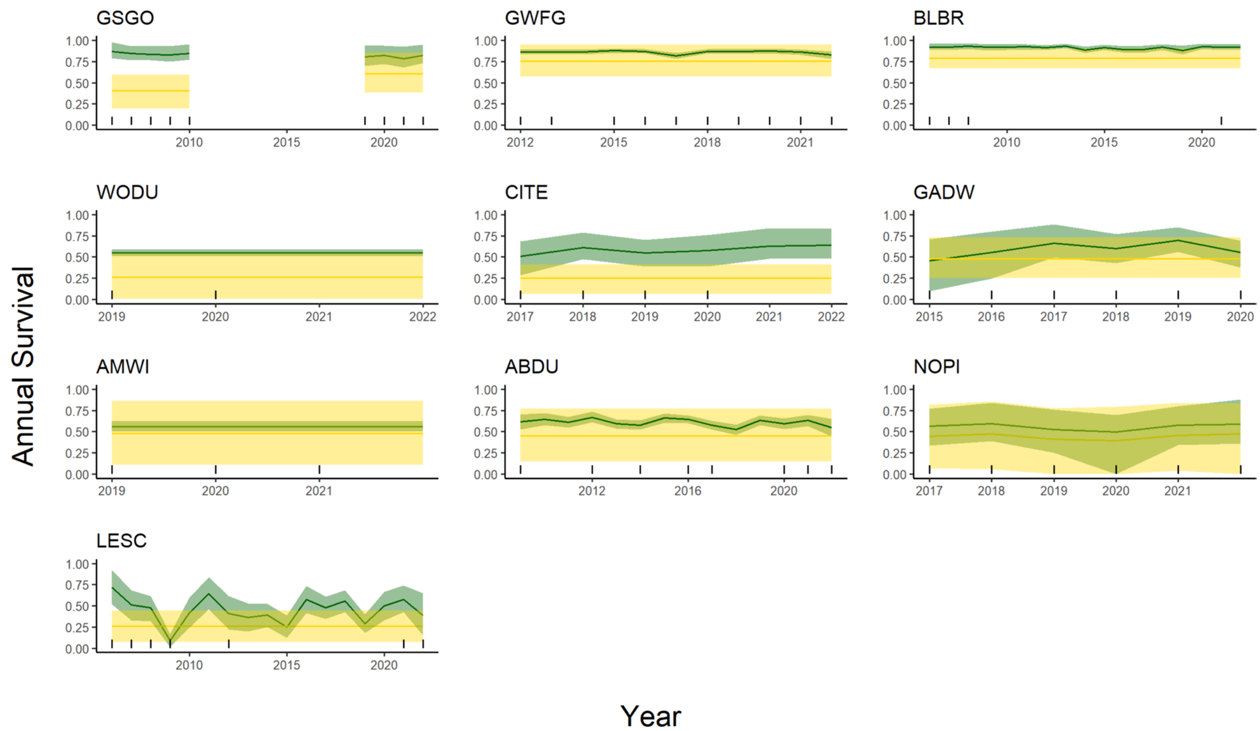

Fig. 3 Time series of adult female annual survival of the ten waterfowl taxa for which survival did not vary by flyway of release. Annual survival of birds fitted with both bands and GPS tags is represented by gold and that of birds fitted only with a metal leg band is represented by green. GSGO = greater snow goose, GWFG = greater white-fronted goose, BLBR = black brant, WODU = wood duck, CITE = cinnamon teal, GADW = gadwall, AMWI = American wigeon, ABDU = American black duck, NOPI = northern pintail, and LESC = lesser scaup. Tick marks on the x-axis indicate years during which GPS tags were deployed on birds

to the metric that indicates the proportion of the posterior on the same side of 0 as the mean (labelled *f*).

Patterns in GPS tag effects on annual mortality across species

To investigate patterns in the effect size of tags on adult female mortality across waterfowl species, we conducted a two-stage analysis. Specifically, we used Bayesian posterior distribution results for effect sizes from the band-recovery analysis described above (level 1), and then examined their relationship with either the pace of species' life histories (fast to slow; level 2) or the body sizes for each species. We quantified effect sizes for each species using the hazard ratio, which we computed as a derived quantity in level 1 of the analysis and indicates the risk of death for individuals wearing GPS tags compared to those wearing only metal bands. This became the response variable in the second stage of the two-stage analysis. Unlike issues of scale that can complicate comparisons of probabilities that are bounded between 0 and 1, hazards ($h = -\log(S)$) alleviate these issues by transformation to a much broader scale (0 to ∞) and are also insensitive to units of time [21]. To consolidate results for each species, we used hazard rates calculated from a log-linear model that accounted for random time effects or other temporal effects, but computed the hazard ratios for use in the second stage of the analysis based on temporal means (i.e. prediction based on an intercept or an intercept and a GPS tag effect). For species supporting geographic variation in hazard rates, we computed hazard ratios using the hazard rate estimates from the Flyway used as a baseline in the model structure (i.e. with the most band releases). For species supporting temporal variation in hazard rates of GPS-tagged birds, we computed hazard ratios using the intercept shared across the two time periods to obtain temporal average hazard rates.

We quantified a proxy of the pace of each species' life history using computed mean life expectancy $= -1/log(S)$, where S represents survival of band-only birds. We also conducted the second stage of the analysis using average body mass (g) of adult females of each species as a predictor of effect size (Table S5), but lacked the data to compare specific mechanisms explicitly as explanatory variables (i.e. we did not have information on individual tag and attachment style, precluding us from evaluating drag or relative weight). As a way to account for one additional metric of life-history strategy, we repeated this analysis using the long-term maximum longevity (as reported by the BBL) of each species and report the results in an appendix.

We fit the following log-linear model in a Bayesian framework to evaluate the relationship between each species' (subscript i) life expectancy and the hazard ratio quantifying the risk of death for individuals wearing GPS tags compared to those wearing only metal bands:

$$\log\left(h_i'\right) \sim \text{normal}\left(\mu_{h,i}, \sigma_{h,i}\right)$$

$$\mu_{h,i} = \gamma_0 + \gamma_1 e_i'$$

$$\log\left(e_i'\right) \sim \text{normal}\left(\mu_{e,i}, \sigma_{e,i}\right)$$

$$\gamma_0 \sim \text{normal}(0, 1000)$$

$$\gamma_1 \sim \text{normal}(0, 1000),$$

where h_i' are posterior draws from the species-specific hazard ratio (i.e. strictly positive values), e_i' are posterior draws from the species-specific adult life expectancy, the μ and σ are the respective means and standard deviations of the estimated parameters from level 1 of the analysis, and the specified priors on γ_0 and γ_1 indicate the mean and the variance. The model therefore propagates uncertainty from stage one of the analysis through stage two [8, 13]. When fitting a similar model with average body mass as a predictor, we did not have the same metrics of uncertainty associated with mass measurements, so e_i' entered into the model as data and line three of the model statement became irrelevant. We include citations for average body mass data of each species in Table S5 .

Results

GPS tag effects on annual survival and mortality

We used records from 300,113 total banded waterfowl and 37,130 total encounters (hunter recoveries). Of these, 2680 bandings and 241 encounters were from individuals marked with both GPS tags and leg bands, and the remaining individuals were marked with leg bands only. Across taxa, the number of GPS-tagged birds that were recovered ranged from 3 to 90, compared with a range of 7 to 20,467 birds fitted only with metal bands (Table 1). Tags reduced annual survival (and increased mortality) of AHY females for all species at some point over the species-specific duration of analysis, and data supported constant survival over time of GPS-tagged birds for all but two taxa (GSGO and CANG; Table 1, Figs. 2, 3). Of the taxa supporting differences in survival between early and late time periods, Canada geese had lower survival in more recent years, indicating stronger effects of GPS devices (Fig. 2). Contrastingly, greater snow geese had considerably higher survival in more recent years, indicating that the effects of GPS devices have been reduced but not eliminated (Fig. 3). The data supported geographic differences in survival by flyway for three of the focal species (Fig. 2, Tables S2 and S6). Hazard ratios computed using the time-averaged hazard rates for both band-only and GPS-tagged birds ranged from 1.13 for LSGO to 3.25 for GSGO, but were also quite high for WODU (2.71), BLBR (2.68), CITE (2.61), LESC (2.34), and CANG (2.26). In addition to LSGO, hazard ratios were on the low end of the spectrum for AMWI (1.58) and MALL (1.45; Table 1). Estimates of band-only survival and conditional recovery were comparable to other estimates found throughout the literature (Table 1 and Table S7).

Life-history patterns in GPS tag effects on annual mortality

Using the time-averaged estimates of GPS tag effects on annual survival and mortality, the interspecific relationship between the mean life expectancy of adult females for each species (which served as a proxy for the pace of a life history) and hazard ratios exhibited a nearly flat relationship ($\gamma_1 = -0.007$, $\sigma_{\gamma_1} = 0.040$, $f = 0.561$; Fig. 4). The interspecific relationship was moderately precise (Fig. 4) despite more precise species-specific results for the vast majority of species (Table 1). The relationship between hazard ratios and body size was similar ($\gamma_1 = -0.07$, $\sigma_{\gamma_1} = 0.16$, $f = 0.670$; Fig. 5), indicating no evidence for a negative relationship.

Discussion

Our study provides insight into the magnitude of negative effects on annual survival (positive effects on mortality) for adult females wearing GPS tags across a spectrum of waterfowl taxa and life-history strategies. The evolved life-history and large body size of long-lived geese should make them more robust to the direct effect of GPS tags on adult survival probability, allowing them to somewhat buffer the effects of wearing tags. However, our results did not support this prediction and instead suggest that effects of GPS tags are consistent across waterfowl species. There remains an inferential tradeoff between the valuable information GPS tags can potentially provide (e.g., detailed individual movement, space use, and other behaviours) and the deleterious effects they can have on survival. Our focus in this study was the interspecific comparison of tag effects rather than the implications of species-specific findings, and future research should experimentally test the effects of GPS tags on each

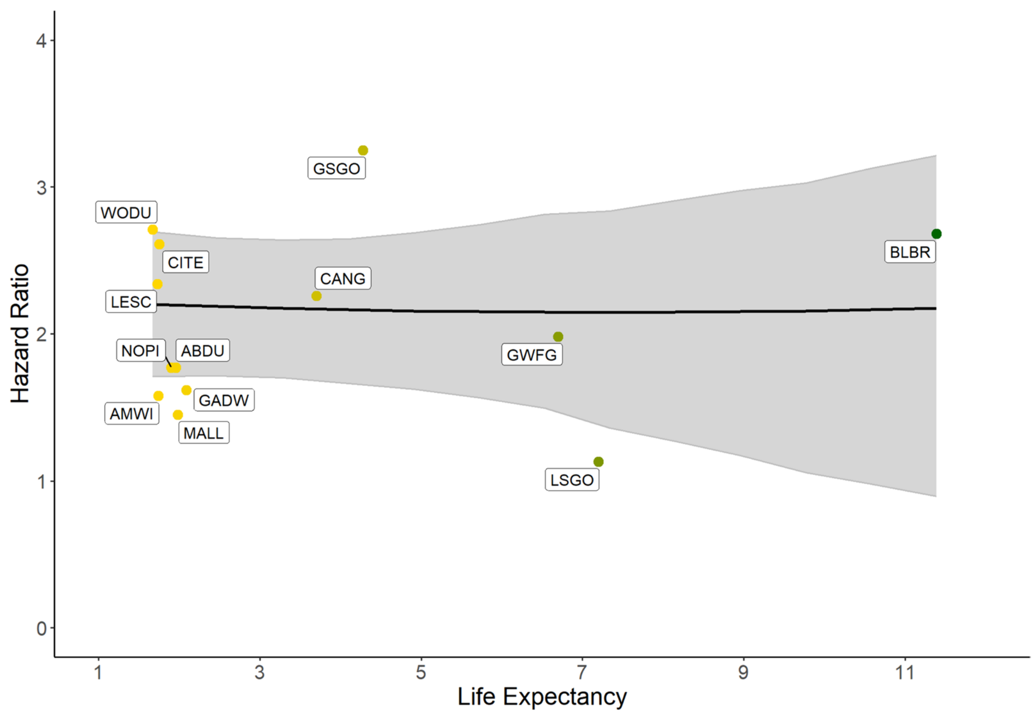

Fig. 4 Estimated relationship between taxon-specific hazard ratios (indicating the risk of death for individuals wearing GPS tags compared to those wearing only metal bands) and taxon-specific adult female life expectancies across 13 waterfowl taxa. For taxa with geographic variation in hazard rates, we used hazard rates from the Flyway with the most precise estimate of band-only hazard rates. Life expectancy, used as an indicator of life-history tempo, is indicated by a color gradient from fast (gold) to slow (green). The bold line indicates the model-predicted mean effect across taxa and the grey shaded region indicates a 90% highest posterior density credible interval

species of concern. Optimistically, however, tag effects on mallard survival, which have been marked with tags more than any other species of waterfowl, were some of the least impactful of any species (though the estimated effect was highly precise; Table 1). Additionally, lesser snow geese appeared to buffer the effects of GPS tags quite well, exhibiting the most similar survival rates between band-only and GPS-tagged birds of any long-lived, large-bodied species.

Seber conditional recovery rates (r; Table S7; [72]) were comparable between GPS-tagged and band-only birds for some species. This suggests that hunting is not the primary cause of higher mortality among GPS-tagged individuals of these species. Recovery rates were higher for seven taxa (GSGO, BLBR, WODU, CITE, AMWI, NOPI, and LESC), however, indicating that tags either make these species more susceptible to harvest, as has been documented for GSGO with neck collars [51], or that hunters report GPS-tagged birds at a higher rate to the USGS Bird Banding Laboratory (i.e. a trophy effect [4]). Of the rate of overall mortality for GPS birds, a greater fraction of it could therefore be from hunting, higher reporting, or a combination. Other than perhaps a neck-collared CANG (a species for which we did not detect a difference in r between GPS-tagged and band-only birds), hunters aren't likely to be able to see the GPS device and thus any greater susceptibility to hunting is more likely related to poor body condition induced by the GPS device (e.g., [22]). The ability to evaluate changes in the magnitude of GPS tag effect size over time is one benefit of incorporating temporal heterogeneity into evaluations of tag effects, and the time variation in band-only survival allows for a more realistic comparison of the two survival rates and whether they have converged over time. The incorporation of temporal variation also yields more precise time-averaged estimates of survival and mortality than if ignored. As sample sizes increase, it would eventually be beneficial to model more complex temporal variation for the sample with GPS tags (e.g., mixed models). Additional advantages of our approach to estimating survival and mortality are that, even when restricting recoveries to only those submitted by hunters, band-recovery models yield asymptotically unbiased estimates of overall survival and mortality [18], and they alleviate the nuance of trying to decouple mortality from tag loss and tag failure based on GPS tag data. The methods we used could also be applied to non-game species that

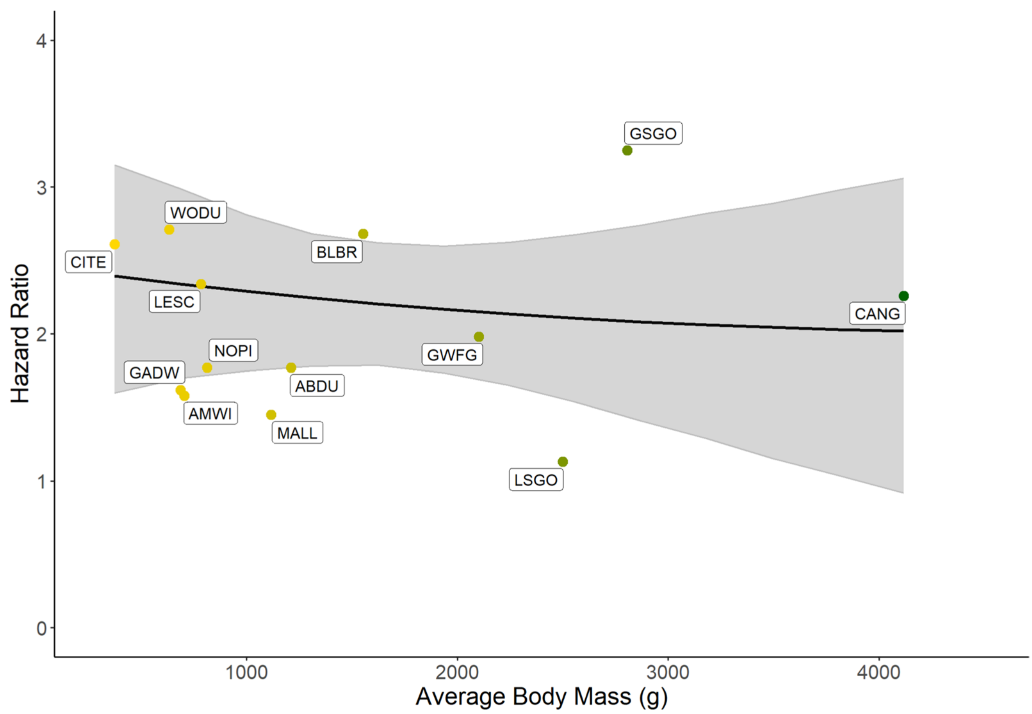

Fig. 5 Estimated relationship between taxon-specific hazard ratios (indicating the risk of death for individuals wearing GPS tags compared to those wearing only metal bands) and taxon-specific adult female body mass across 13 waterfowl taxa. For taxa with geographic variation in hazard rates, we used hazard rates from the Flyway with the most precise estimate of band-only hazard rates. Life expectancy, used as an indicator of life-history tempo, is indicated by a color gradient from fast (gold) to slow (green). The bold line indicates the model-predicted mean effect across taxa and the grey shaded region indicates a 90% highest posterior density credible interval

are recaptured or recovered as a simple way to evaluate tag effects across more taxa [16].

The mechanisms responsible for reductions in survival may be relatively similar across species, regardless of the magnitude of effect size. Given that annual survival is an umbrella vital rate that represents the chance of surviving all possible causes of mortality and is intricately linked to other demographic parameters via life-history tradeoffs, it is worth considering how tags might affect other demographic parameters and traits associated with them [43, 49, 58, 80]. The sub-lethal effects of GPS tags may be difficult to account for, and information remains unavailable about the magnitude of these effects across a broad range of species (but see [6]). Behavioural changes have been noted in many species affixed with GPS tags, from increased preening and vigilance behaviours to impaired locomotion [29, 36] and avoidance of conventional habitat preferences, which may reduce body condition due to limited food access [22, 40]. Depending on the attachment style used, feather and skin abrasions may result from rubbing of the tag or the associated harness, potentially resulting in infection [47]. Among game species, auxiliary markers may make birds more visible and more easily targeted by hunters [73] or predators [75], may impair birds by collecting ice on the device [23], or impaired body condition may induce them to more readily decoy and be harvested [2]. Additionally, GPS tags may be particularly impactful to survival during specific life-history events such as migration where increased weight, decreased aerodynamics, and potential for ice formation may combine to reduce survival during long-distance and high-elevation movements. For example, median mortality rates across multiple species during both fall and spring migration were 4.4 times higher than during stationary periods, and effects during spring migration were more pronounced (6.3 times higher than stationary periods) than during fall migration (3.0 times higher than stationary periods [60],).

Research into the specific mechanisms driving tag-related reductions in survival is warranted and may aid in mitigating specific impacts resulting from attachment style, tag design, or tag weight. In particular, further research into specific attachment methodology used on Canada geese should take priority, given signals that they may have experienced increasing tag effects over time (Fig. 2). For researchers studying geese that are large enough to wear new lightweight neck collar GPS tags, detailed research on GSGO provides valuable insight into the possible information gains but also caution that is warranted when deciding about the use of these styles of attachment [9, 17, 50]. Though field-readable plastic neck collars did not historically induce a mortality effect on the large and robust GSGO, enhanced hunting pressure has increased both the hunting and non-hunting mortality of individuals wearing neck collars compared to individuals wearing only metal bands [51]. We were able to evaluate changes in the survival of birds fitted with GPS tags over time, but we could not statistically detect a temporal change in tag effects for most species (Figs. 2 and 3). Some research has shown decreased impacts from implanted tags in dabbling ducks compared to other attachment styles [3, 63, 76], although such tags still appear to cause a handicap in at least some diving ducks [45]. Future research into attachment styles and specific inquiry into possible effects of collar-based tags is warranted [51], and new attachment styles might be considered as technology advances and device size decreases (e.g., auxiliary leg bands).

Our study synthesizes multiple species, geographic regions, life-history strategies, body sizes, and band-recovery data to result in a cohesive message of caution to wildlife researchers and managers. Future studies drawing inference from birds fitted with GPS tags should consider whether or not those birds are representative for objectives pertaining to demography, ensure they are transparent regarding any negative effects related to the tags [10, 19, 25], and attain sample sizes that are robust enough to test for such effects [53]. Given that they are such useful and widely used tools, we do not expect the use of GPS tags to diminish in the coming years and we acknowledge the important contributions their use has provided to the field of avian ecology. These contributions include detailed insights into movement and habitat use [41, 55], disease ecology [56, 78], and human–wildlife conflicts (e.g., real-time adaptive management of aeronautics in response to bird activity near airports, [5, 15, 32]. It is nevertheless important that future experimental design allows for the evaluations of tag impacts on birds so they can be accounted for when interpreting results. Arranging study control groups for comparison with individuals fitted with tags will allow for the evaluation of effects, and being mindful that the censoring of individuals should be random with respect to the outcome of interest will result in less biased estimates of tag effects on survival going forward [74].

Replication of our study is warranted as additional harvests of tagged birds occur and as more GPS tags are deployed. Future studies should verify the magnitude of marker effects across species as technology hopefully leads to less intrusive devices. Those studies might also attempt to experimentally decouple the effects of life-history strategy and body size, which are often closely scaled with one another, and which we could not explicitly do here [1]. Being mindful of assumptions about random censoring, known-fate evaluations of GPS tag effects on cause-specific mortality are also needed in systems where study design allows for such insights, and can overcome the missing-bird dilemma in large-scale studies of long-distance migrants [74]. This might be especially needed for GSGO and NOPI. After several decades of observation, researchers have found that simple plastic neck collars (~ 15 g) interact with hunting intensity among GSGO to reduce absolute survival by approximately 0.12 (95% CI 0.09, 0.15 [51],) and have observed a reduced lifespan for individuals fit with even heavier modern GPS neck tags (~ 45 g). Hunters may be reluctant to report shot GPS-tagged birds for fear that researchers may force them to return the tags which are generally regarded as trophies in the hunting community (LeTourneux & Legagneux, personal observation). This suggests that some of the survival estimates in this study associated with GPS-tagged birds may be biased high. In other species, some of the results we found are likely to be conservative, especially if birds that die very quickly after GPS tag deployment are removed from the sample (and practitioners put the tag on another individual, for example). Gadwall are potentially one species for which this occurs somewhat frequently (Setash, personal observation), which may explain the similarity in survival between band-only and GPS-tagged birds (Fig. 3). Alternatively, tag deployment right before the start of the hunting season may give birds less time to get used to GPS devices, and a band recovery model may bias survival low (i.e. they are immediately subject to the impact of hunting after being fit with a new device). Therefore, in migratory bird systems where mortalities can be accurately deciphered from tag failure and tag loss, we highly encourage the application of known-fate survival models (e.g., the common Cox proportional hazard) to the GPS track and fate data to address these potential issues as well as more detailed spatio-temporal questions. Future studies might also benefit from assessing lagged tag effects in long-lived species to see whether tag effects are delayed and may result in premature senescence [35]. With respect to important vital rates such as survival and mortality, GPS tags are not yet entirely benign, despite a considerable effort among practitioners to minimize effects. Efforts should therefore be made to mitigate, report, and interpret effects accordingly in future studies. Managers may therefore be warranted in remaining cautious about inferences regarding population demography from GPS tag studies and should understand resulting biases when informing conservation and management actions.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-024-00381-2.

Supplementary file 1 Table S1: Assignment of geographic/administrative Flyways used to separate banding data of waterfowl across North America. Region codes in the original data indicated states and provinces listed in the left column, and we assigned Flyways as indicated for each region. Table S2: Final model structure for each species. Temporal variation indicates whether mortality of birds with GPS tags was divided into an early or late period or constrained to be constant across the study period. Geographic variation indicates whether and which flyways were allowed to differ in mortality of both band-only birds and GPS-tagged birds. The flyway in parentheses indicates the baseline/intercept, whereas the other flyway listed had an offset in the model structure. An "&" in between flyways indicates that those flyways were constrained to have the same survival, but differed from the other flyway listed (see Fig. 2 in manuscript). Table S3: Survival estimates used to create informed priors in species-specific dead recovery models of waterfowl. Literature cited is listed below the table. Table S4: Informed priors used to evaluate annual survival of AHY females of 13 waterfowl species. Survival estimates were based on published estimates in Table S3 and moment matched to obtain alpha and beta parameters in the far-right column. Table S5: Average body mass (g) of each waterfowl taxon used as a predictor of effect size (hazard ratio) in stage two of the analysis and respective citations for each measurement. Table S6: Annual survival estimates of AHY females that supported geographic differences. We report band-only and GPS tag survival for each Flyway combination. Table S7: Conditional recovery probability estimates (which are not proportional to direct recovery rates) from the Bayesian band recovery model for 13 species and sub-species of waterfowl fitted with only a metal band or also with a GPS tag. These included lesser snow goose (LSGO), greater snow goose (GSGO), greater white-fronted goose (GWFG), black brant (BLBR), Canada goose (CANG), wood duck (WODU), cinnamon teal (CITE), gadwall (GADW), American wigeon (AMWI), mallard (MALL), American black duck (ABDU), northern pintail (NOPI), and lesser scaup (LESC). Figure S1: Testing for effect of maximum longevity of a species on the GPS tag effect size. Effect size is measured by hazard ratio of mortality of GPS-tagged birds to mortality of band-only birds. Approximately 79% of the posterior distribution of the regression coefficient for this relationship was negative (-0.11, SD = 0.13), indicating a lack of a significant negative relationship. (DOCX 70 KB)

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Author contributions
All authors conceived the main ideas. C.M.S and A.C.B formatted the data used in analyses. C.M.S and D.N.K conducted analyses and wrote the manuscript. J.H.G, A.C.B, and B.Z.L contributed editorially to the manuscript. M.L.C, C.T.O, B.Z.L, F.E.B, K.E.B, N.R.H, P.L, and M.L.S contributed data to the analyses and to important editing of the manuscript.

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Data availability
Data are archived by the USGS Bird Banding Laboratory (BBL), Laurel, MD, USA, and have been used in accordance with USGS BBL policy provided in the GameBirds database. Data collected after 2019 by researchers and managers who expressed concern regarding the inclusion of those data were excluded from all analyses (10 teams in total).

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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