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Methodology

Detecting capture-related mortality in radio-marked birds following release

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ABSTRACT. A fundamental assumption of avian survival analysis is that the act of capture, handling, and marking birds does not affect subsequent survival. This assumption is violated when animals experience injury, physiological stress, or disorientation during capture and handling that increases their mortality risk following release. Such capture-related effects must be accounted for during analysis, typically by censoring individuals from the survival history, to avoid biasing the resulting survival estimates. We reviewed studies of radio-marked upland game birds to characterize researcher approaches for addressing short-term effects of capture on survival, and used data from a study of Ruffed Grouse (*Bonasa umbellus*) to illustrate an empirical approach for evaluating such effects and identifying time thresholds to censor individuals that die shortly following release. A majority of studies (65%) reported using some form of censoring for mortality that occurred within one to three weeks after release, although only 8% of studies reported an empirical approach to identify a threshold for censorship. We found that Ruffed Grouse mortality was greater from one to six days following release when compared with 7 to 30 days. This threshold, and the proportion of birds censored as a result of it, is consistent with a number of previous studies of radio-marked Ruffed Grouse. We also found that short-term mortality of Ruffed Grouse following release was reduced by checking traps twice each day and by adequately concealing traps. We recommend that future studies of radio-marked birds employ empirical methods for detecting postrelease mortality thresholds, which will allow for reduced bias while minimizing unnecessary censorship of birds that die for reasons unrelated to capture.

Détection de la mortalité attribuable à la capture chez des oiseaux marqués par radiotélémétrie

RÉSUMÉ. L'analyse de la survie des oiseaux repose sur l'hypothèse de base voulant que l'acte de capturer, manipuler et marquer des oiseaux n'affecte pas leur survie subséquente. Cette hypothèse est violée lorsque les animaux subissent des blessures, un stress physiologique ou une désorientation pendant la capture et la manipulation, puisque leur risque de mortalité une fois relâchés augmente du coup. Ces effets imputables à la capture doivent être considérés au moment des analyses, en suivant habituellement l'histoire de survie des individus, afin que les estimations de la survie ne soient pas biaisées. Nous avons passé en revue des études réalisées sur des oiseaux terrestres considérés comme gibier afin de caractériser les approches utilisées par les chercheurs pour tenir compte des effets à court terme de la capture sur la survie. Nous avons également utilisé les données d'une étude sur la Gélinotte huppé (Bonasa umbellus) afin de présenter une approche empirique destinée à évaluer ces effets et à déterminer les seuils temporels où on devrait interrompre le suivi des individus qui meurent rapidement une fois relâchés. La majorité des études (65 %) rapportaient avoir interrompu de diverses façons le suivi d'individus dont la mortalité était survenue à l'intérieur d'une à trois semaines après la remise en liberté, mais on rapportait avoir utilisé une méthode empirique pour déterminer un seuil pour cette interruption de suivi dans seulement 8 % des cas. Nous avons constaté que la mortalité des gélinottes était plus élevée dans la période allant du 1er au 6e jour suivant leur remise en liberté, que dans la période allant du 7e au 30e jour. Ce seuil, et la proportion d'oiseaux dont le suivi a été interrompu en fonction de celui-ci, concordait avec bon nombre d'études antérieures dans lesquelles des gélinottes étaient marquées par radiotélémétrie. Nous avons aussi trouvé que la mortalité survenant à court terme une fois les gélinottes relâchées était réduite si l'on vérifiait les trappes deux fois par jour et si l'on camouflait celles-ci adéquatement. Nous recommandons que les études futures sur des oiseaux marqués par radiotélémétrie utilisent des méthodes empiriques pour déterminer les seuils de mortalité après remise en liberté, ce qui permettra de réduire les biais tout en minimisant les interruptions non nécessaires dans le suivi des oiseaux qui meurent pour des raisons non liées à la capture.

Key Words: *capture effects; galliform; game birds; mortality; radio-telemetry; Ruffed Grouse; survival*

INTRODUCTION

Many aspects of avian biology, such as breeding behavior and habitat use, influence mortality risk and thus affect population dynamics. These processes are illuminated through survival analysis (Murray 2006, Murray and Patterson 2006, Sandercock 2006), which seeks to both quantify rates of period-specific survival and to evaluate sources of variation in mortality risk among individuals. Most survival studies involve physical capture, handling, and marking of birds, with some notable exceptions, e.g., genetic mark-recapture. All such studies

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implicitly assume that mortality risk to marked individuals is representative of the population as a whole (Pollock and Raveling 1982, Esler et al. 2000, Murray 2006). This assumption may be violated if the act of capturing, handling, and/or marking a bird increases its mortality risk following release, in which case estimates of survival are biased low. Evaluating this potential bias, and if necessary accounting for it, are therefore important components of avian survival research.

Numerous studies have addressed potential effects of capture and marking on individual species (e.g., Esler et al. 2000, Dugger et al. 2006, Hagen et al. 2006, Holt et al. 2009, Gibson et al. 2013), and a number of synthesis reviews have been published for both birds (e.g., Calvo and Furness 1992, Barron et al. 2010) and animals in general (e.g., Murray and Fuller 2000). Deleterious effects of capture and marking can be separated into two discrete categories: effects that are short term and acute, and effects that are long term and chronic (Holt et al. 2009). Long-term effects are normally associated with reductions in annual survival or behavior attributed to carrying the mark itself. For example, if the attachment of a radio-collar impacts behavior, thus altering potential breeding success (e.g., Gibson et al. 2013, Fremgen et al. 2017). Evaluating long-term effects normally requires an experimental design using multiple marking techniques (e.g., radio-marked vs. banded-only; Barron et al. 2010). Short-term effects, in contrast, may result from a variety of factors associated with capture, handling, and/or marking. Following release, a bird may succumb to injuries (either observed or latent) that were incurred during capture (Grisham et al. 2015), may die as a result physiological complications due to capture and handling, i.e., capture myopathy (Arnemo et al. 2006), or may die via indirect causes, such as predation, that occur because the bird is disoriented after release or is acclimating to presence of the mark. Hereafter we will use the term capture effects to refer to this suite of potential short-term impacts associated with capture, handling, marking, and release.

Understanding capture effects can be challenging for studies informed solely by live observations, e.g., live recapture or band reading (Sandercock 2006), where mortality itself is rarely observed. Radio-telemetry studies differ in that both live and dead status are used to inform survival estimates (Murray 2006), thus offering an ability to evaluate timing of death relative to release and infer whether death may have been related to capture. This in turn presents a series of decision points to researchers, where they must choose whether or not to remove individuals that die shortly after release from the survival history, i.e., left-censoring, and if so, what amount of time must pass before mortality is presumably not associated with capture. The approaches used are variable among researchers, and are often determined subjectively, despite that empirical evidence from data can be used to inform the decision process (Holt et al. 2009). If capture effects exist, survival probabilities should be lower immediately following release but increase predictably through time, and these temporal patterns should be detectable using standard approaches to survival analysis and appropriate time scales.

Our objective for this research was to summarize the range of approaches used by researchers when addressing capture effects on survival during radio-telemetry studies, and to present a systematic method for detecting thresholds of postrelease mortality to better-inform future work. We reviewed recent (2006–2017) literature from studies of upland game birds to characterize contemporary approaches to this issue, and we expected that the majority of researchers would use arbitrary time thresholds for left-censoring birds, or would not censor birds at all. We chose to focus our review on game birds because they are often studied using radio telemetry, and tend to share a similar suite of methods for capture and marking across species. We then used data from a three-year study of radio-marked Ruffed Grouse (*Bonasa umbellus*), a widely distributed gamebird in North America that has been the focus of numerous telemetry studies (Small et al. 1991, Gutierrez et al. 2003, Yoder et al. 2004, Devers et al. 2007, Skrip et al. 2011), to illustrate a data-driven approach to evaluate capture effects and thresholds of postrelease mortality. Here, we approached the analysis with an a priori hypothesis that realized thresholds in postrelease mortality would match those commonly cited in Ruffed Grouse research. Our work compliments and expands on prior similar assessments (e.g., Holt et al. 2009) by incorporating more recent literature and a broader suite of species, as well as by using an expanded suite of analytical tools for detecting threshold effects from radio-telemetry data.

METHODS

Literature review

We conducted a review of upland game bird survival studies to quantify the frequency at which researchers used differing methods for addressing capture effects on survival. We focused our review on publications that used radio-telemetry to detect mortality and estimate survival. Although this constraint excluded studies that used other methods to estimate survival, e.g., banding and capture-mark-recapture, we presumed that detection of immediate postrelease mortality was unlikely in most such studies because they rely on live detections, or are based on hunter recoveries, of marked birds. We conducted our search with Google Scholar (https://scholar.google.com/), using combinations of the following key words: radio telemetry; survival; grouse; prairie chicken; quail; bobwhite; wild turkey. We restricted our review to peer-reviewed articles published in journals or as symposia proceedings from the period 2006 to 2017. We did not consider earlier works in part to narrow our search window, which made the review more practical while still generating a substantive sample of published work. More importantly, our use of this date range ensured a review of contemporary studies that best reflected current practices, both field and analytical. See Holt et al. (2009) for a similar review and evaluation of earlier works specifically related to Northern Bobwhite (*Colinus virginianus*). Our intent for this exercise was not to produce an exhaustive review of the literature on this subject, but rather to generate a sample of studies that was sufficiently large to be representative of the approaches used by game bird researchers.

For each paper, we recorded the study species and classified the approach to postrelease censorship into one of four categories: (1) investigators did not censor any mortalities, (2) censored based on field evidence that suggested cause of death was related to capture, (3) censored based on an a priori time threshold, or (4) censored after using a post hoc assessment of the appropriate time threshold. If a paper did not explicitly report any approach to censoring, we assumed that category 1 (did not censor) was the approach used. For category 3 (a priori threshold) we further distinguished among studies that censored all individuals prior to the threshold date, i.e., delayed entrance into the survival history, and studies that only censored individuals that did not survive the censor period. The distinction between these two approaches is that surviving birds contributed data to survival estimates during the censor period in the latter approach, but not the former. We recorded the threshold length in days for each study, and also recorded the proportion of captured birds that were censored from the analysis when the information provided in the paper allowed for it. In all cases we focus exclusively on censoring of bird deaths that occurred shortly (< 30 days) following release that were potentially associated with capture. Many studies describe truncation of survival histories, i.e., right-censoring (Murray 2006) because of other factors such as transmitter failure or emigration from the study area, and those approaches were not the purpose of our review. Moreover we did not consider handicaps associated with long-term effects of radio-marking in this study, which have been reviewed elsewhere (Barron et al. 2010).

Example application

Field methods

We captured Ruffed Grouse in two study areas in central Maine, USA, during 2014–2016. Our capture season consisted primarily of the months of August and September, although we trapped a few birds during October, April, and May. We used modified lily-pad traps following Gullion (1965) that were similar in design to those used in most other recent Ruffed Grouse research (Devers et al. 2007, Skrip et al. 2011). Traps normally consisted of two round trap bodies constructed of welded wire and covered with a piece of mesh fabric, which were connected by an approximately 20 m long wire drift fence that lead into one-way wire funnels. We checked traps once each day immediately before sunset during 2014, and in 2015 and 2016 we increased our trap check frequency to two times each day, with the additional check occurring during midmorning, approximately four hours after sunrise. Evening checks were intended to prevent birds from remaining in traps overnight, and late morning traps were intended to reduce the length of time birds spent in traps if they were captured early in the day. All traps were concealed by piling natural debris, e.g., branches and leaf litter, on top of the trap, and in 2015 and 2016 we increased the level of concealment by piling substantially more materials on and around the sides of the trap body. Both of these modifications were designed to reduce the risk of self-inflicted injury to captured birds; more frequent trap checks reduced the amount of time a bird spent in the trap body following capture, and increased concealment was intended to improve the birds' sense of security while in the trap. We determined age of each captured bird as hatch-year (< 1 year of age) or after-hatch-year (> 1 year of age) and sex based on feather characteristics (Davis 1969). All birds were fitted with an aluminum leg band and a 12-g-radio transmitter with a necklace-style attachment, which featured a mortality sensor that increased the radio signal pulse rate when the collar remained motionless for > 8 hours, and we did not radio-mark individuals weighing ≤375 g. All capture and handling of Ruffed Grouse was approved by the Institutional Animal Care and Use Committee at the University of Maine (IACUC Protocol A2014-03-06).

We monitored all radio-marked Ruffed Grouse using hand-held radio receivers every one to three days for the first 30 days following release, and recorded and investigated mortalities when they occurred to confirm the bird had died. We relied strictly on the radio signal for monitoring and did not flush or otherwise disturb birds after release, unless they were recaptured. Both the radio collar and leg band were printed with a toll-free phone number for hunters to report marked Ruffed Grouse to the University of Maine if they were harvested during the hunting season, which began 1 October during each study year. Some of our mortality data reflected harvest that occurred within 30 days of capture, and we did not distinguish between harvest and nonharvest mortality for the purpose of this study.

Data analysis

We analyzed daily survival probabilities of radio-marked Ruffed Grouse using nest survival models, implemented in Program MARK (White and Burnham 1999) via the R (R Core Team 2017) package RMark (Laake 2016). We distilled our monitoring data into individual survival histories for each radio-marked bird, where day 1 of the history reflected the day of capture, rather than the calendar date, i.e., all histories began on day 1. Sometimes a Ruffed Grouse was captured > 1 time within a single trapping season, in which case we right-censored the bird's original history on the day prior to its subsequent capture, and began a new history (as day 1) that reflected the time elapsed since the second capture. In cases where we lost radio contact with a bird, e.g., due to a radio malfunction, we right-censored that bird from the survival history following the last day we obtained a signal from it. All histories were truncated 30 days after capture, which we chose as an end point for this analysis because we were interested exclusively in short-term effects of capture; using a time period of greater duration could potentially confound results with other longer term temporal processes that were unrelated to capture, e.g., seasonal variability.

We approached our analysis in two phases. During the first phase, we tested for and identified potential sources of heterogeneity in survival that that were not explicitly tied to capture effects. These included year, bird age, bird sex, study area, and date of capture. We included the ordinal date of capture in the analysis to account for the possibility of seasonal changes in survival, given that our primary capture period spanned two calendar months. Year was potentially informative, with respect to capture effects, because of the changes we implemented in trapping protocols between our first and second/third study years. We constructed single term models based on each of these five variables, and compared them against each other and a null model (intercept only). In all analyses we made comparisons among models using AIC_c (Anderson and Burnham 2002), where we considered models to have similar support when they fell within 2.0 AIC_c units of a contrasting model, e.g., the null model. We also examined confidence intervals around parameter coefficients, and gauged parameter support based on whether 95% confidence intervals overlapped 0.0.

In our second phase of analysis, we included all variables supported during phase 1 as a base model structure, and then considered time effects on postrelease survival that took one of three forms. First, we considered a model where we allowed full independence in survival probability among each of the 30 days postcapture. Although this model was highly parameterized and thus unlikely to be competitive based on AIC_c, it was nevertheless important because it allowed us to visualize the full range of variability in daily survival probabilities independent of any modeled constraints. Second, we fit three forms of models that were intended to reflect systematic temporal trends in daily survival postrelease; these models included both linear and quadratic trends on daily survival probability, as well as a model where we applied a natural log transformation to the numeric value of days postrelease. This later model form produced a nonlinear pattern that was similar to the quadratic model, but has the added benefit of not forcing nonlinear trends at both minimum and maximum values for the predictor variable, as can often happen with a quadratic effect. Collectively these models were designed to test for systematic increase in daily survival throughout the 30-day postrelease period, which would be indicative of a generally diminishing effect of capture and marking. Finally, we explored a series of models where we specified a threshold point in which the daily survival probability was allowed to vary before and after the threshold, but where within the respective time intervals on either side of the threshold survival was constant. These models allowed us to test for shifts in survival that were indicative of the most appropriate threshold date to use when censoring postrelease mortalities. We constructed one model for each potential threshold, beginning with day 2 and continuing through day 29. Although this approach results in a relatively large number of models, it also selects a threshold in postrelease survival that is both explicit and empirically defined. In contrast, for models that allow full independence in survival estimates, or that force constrained trends, thresholds must be interpreted qualitatively based on patterns in the resulting survival estimates.

For the second phase of analysis we made two assessments of model selection results, one in which we evaluated the whole suite of models to identify the best-supported temporal structure, and a second where we compared results among only the threshold models. We used criterion for model selection and variable importance as described above, and we also calculated AIC_c model weights (w_i; Anderson and Burnham 2002) from among only the subset of threshold models to aid in interpretation of threshold timing. We used both model deviance and w_i to evaluate relative support among competing threshold value models; deviance was appropriate for model selection in this specific case because all threshold models shared a common number of parameters. Finally we computed an R^2_Dev statistic as

$$R^2Dev = \frac{Dev_{Null} - Dev_{covariate}}{Dev_{Null} - Dev_{Full}} \quad (1)$$

which yields an approximation of the proportional temporal variance that is explained by a time-structured covariate (Grosbois et al. 2008). In our case, the null model contained the base model structure with no within-year temporal variation. The full model allowed full daily variability in postrelease survival, and the covariate of interest was our best-supported threshold model.

RESULTS

Literature review

We reviewed 58 publications representing 12 species of upland birds (Table A1.1). Two of these publications contained two distinct analyses, and so our review consisted of 60 total survival analyses. Sixty-five percent of studies (n = 33) applied one of the three censoring criteria to birds that died postrelease, whereas 45% of studies (n = 27) did not report censoring postrelease mortalities. The most common approach to censoring involved use of an a priori censoring period, which was applied in 35% of studies (n = 23). Among studies using this approach, most removed birds from analysis that died prior to the postrelease date threshold (n = 17), whereas in a smaller number of studies (n = 6) authors reported withholding all birds from survival histories until they passed the date threshold. Censoring that was based on field evidence (n = 5), and systematic approaches to detect postrelease survival thresholds (n = 5), each were represented by 8% of studies. The length of censoring periods among studies that incorporated them (either a priori or systematically derived) ranged from 1 to 21 days, with a mean of 9.1 days postrelease. Only 11 studies reported sufficient information to calculate the proportion of individuals that were censored because of post-release mortality, and those values ranged from 0.015 to 0.160, with a mean of 0.074.

Survival analysis

We captured and radio-marked 294 individual Ruffed Grouse, and recorded 56 mortalities that occurred during the first 30 days after release. Our first stage of analysis identified study year and bird age as important predictors of postrelease survival, whereas date of capture, study area, and sex were not related to survival (Table 1). Survival was lowest following releases that occurred during the first year of our study, whereas survival was greater during the second (β = 0.65; 95% CI = 0.03 to 1.27) and third years (β = 0.84; 95% CI = 0.03 to 1.66). This resulted in an approximately 0.006 increase in the average daily survival probability during years 2 and 3, compared to year 1. The single-term age model was within 2.0 AIC_c of the null model, and suggested that daily survival of hatch-year birds was reduced by approximately 0.003 compared to after-hatch-year birds. However, 95% confidence intervals of the coefficient overlapped 0.0 (β = -0.36; 95% CI = -0.90 to 0.17) and so support for the age effect was not equivocal. We nevertheless elected to retain the age effect, along with the year effect, in the second stage of analysis, because independent analysis of our larger telemetry dataset for this system demonstrate clear differences in survival among age classes (Davis 2017).

In our second stage of analysis we found the greatest support for a survival threshold that occurred between six and seven days following release (Fig. 1). The second-most support was for a model that identified a threshold between days 10 and 11, however this model was 2.53 AIC_c units from the day 6 threshold model, and thus was not competitive based on our criterion of 2.0 AIC_c (Table 1). The day 6 threshold model also had the lowest model

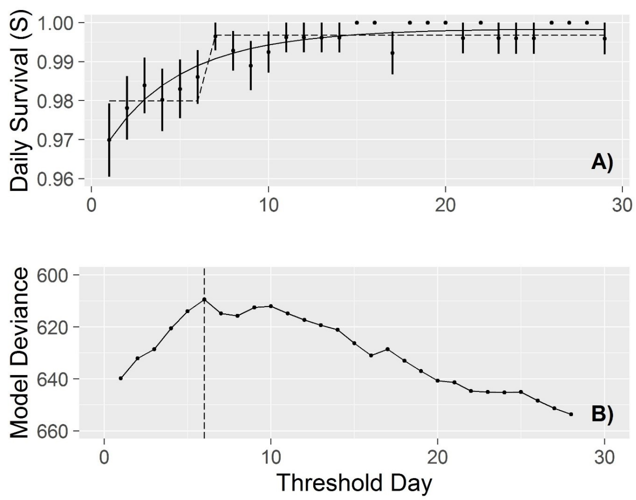
Table 1. Model selection results for nest survival analyses that describe the daily survival probability of Ruffed Grouse (*Bonasa umbellus*) for the first 30 days following release and radio-marking. Models were implemented in Program MARK using the R package RMark (Laake 2016). Temporal models took one of three forms: a model allowing full daily variation, daily trend models (linear, quadratic, natural log), and a series of models identifying discrete threshold points of postrelease mortality.

Model†	AIC_c	ΔAIC_c	K	Deviance
Quadratic Trend + Base	615.14	0.00	6	603.13
Linear Trend + Base	615.92	0.78	5	605.91
LN(Day) + Base	617.31	2.17	5	607.30
Day 6 + Base	619.50	4.35	5	609.49
Day 10 + Base	622.02	6.88	5	612.02
Day 9 + Base	622.48	7.34	5	612.48
Day 5 + Base	623.99	8.84	5	613.98
Day 7 + Base	624.80	9.65	5	614.79
Day 11 + Base	624.85	9.71	5	614.84
Day 8 + Base	625.78	10.64	5	615.77
Day 12 + Base	627.29	12.14	5	617.28
Day 13 + Base	629.37	14.23	5	619.37
Day 4 + Base	630.55	15.40	5	620.54
Day 14 + Base	631.15	16.01	5	621.15
Day 15 + Base	636.31	21.17	5	626.31
Day 3 + Base	638.64	23.49	5	628.63
Day 17 + Base	638.64	23.50	5	628.63
Day 16 + Base	641.01	25.86	5	631.00
Day 2 + Base	642.09	26.95	5	632.09
Day 18 + Base	643.01	27.87	5	633.00
Day 19 + Base	647.04	31.89	5	637.03
Day 1 + Base	649.76	34.62	5	639.75
Day (full) + Base	649.94	34.80	32	585.67
Day 20 + Base	650.73	35.58	5	640.72
Day 21 + Base	651.33	36.19	5	641.32
Day 22 + Base	654.65	39.51	5	644.65
Day 25 + Base	655.04	39.89	5	645.03
Day 23 + Base	655.09	39.94	5	645.08
Day 24 + Base	655.28	40.14	5	645.28
Day 26 + Base	658.40	43.26	5	648.39
Day 27 + Base	661.39	46.25	5	651.38
Base	662.08	46.94	4	654.08
Year	662.80	47.66	3	656.79
Day 28 + Base	663.67	48.53	5	653.66
Null	665.95	50.81	1	663.95
Age	666.15	51.01	2	662.15
Date of Capture	666.52	51.37	2	662.51
Sex	667.49	52.35	2	663.49
Study Area	667.88	52.73	2	663.87

† All time-structured models (full daily variation, day thresholds, trends) included a base model structure that contained variables supported during a first stage of analysis (Year + Age). Year = fixed effect of study year (2014, 2015, 2016); Age = Hatch Year vs After Hatch Year; Date of Capture = the ordinal date of year that the bird was captured; Sex = Male vs Female; Study Area = survival allowed to vary among two study areas. LN(Day) reflects a natural log transformation of the number of days postcapture.

deviance (Fig. 1), and among all threshold models had an AIC_c weight (w_i = 0.55) that was 3.5x greater than the day 10 model (w_i = 0.15). When averaged across years and age classes, this model suggested the mean daily survival probability during the first six days following release was 0.980 (±0.003 SE), and for days 7 through 30 the mean daily survival was 0.997 (± 0.001 SE).

Fig. 1. Daily survival probabilities (A) and model deviance (B) from analysis of radio-marked Ruffed Grouse (*Bonasa umbellus*) survival during the first 30 days following release. For panel A, point estimates of daily survival (error bars reflect 95% confidence intervals) were derived from a model allowing full independence among daily estimates. The solid line reflects a quadric trend in daily survival, and the dashed line represents a model that identified a threshold in mortality that occurred between days 6 and 7. Panel B represent differences in model deviance among all potential daily thresholds for postrelease mortality. The y-axis is inverted, and smaller deviance values indicate better fit, where the best-fit model is indicated by the dashed vertical line. All models were ran as nest survival analyses, implemented in Program MARK (White and Burnham 1999) using the R package RMark (Laake 2016).



However, models that included linear trends, quadratic trends, and a natural log transformation of day were better-supported than the most competitive threshold model, with the greatest support for the quadratic trend (Table 1).

When comparing trend- and threshold-based estimates with those from a model that allowed for independent estimates across the entire 30-day postrelease period, it was apparent that support for the quadratic trend was driven in large part by a systematic increase in survival during the first six days postrelease, where survival was lowest during the first 24 hours and increased progressively thereafter (Fig. 1). The six-day threshold model explained approximately 65% of the temporal variance in postrelease survival (R^2_Dev = 0.65), and the quadratic daily trend model explained an additional 9% (R^2_Dev = 0.74).

DISCUSSION

We found that approaches to addressing capture effects differed among investigators. Although our review allowed us to quantify standard practices, there were additional differences that were more subtle and difficult to characterize with a formal review. The majority of researchers applied some sort of a censoring protocol to account for capture-related mortality, however specific strategies used, and whether censoring was employed at all, varied somewhat among species. For example, 9 of 14 studies that we reviewed on Greater Sage-Grouse (*Centrocercus urophasianus*) reported no censoring criteria, and those that did were often focused on radio-marked chicks and censored individuals based on field evidence that suggested capture effects (Gregg and Crawford 2009, Dahlgren et al. 2010, Guttery et al. 2013). In contrast, all five studies of Wild Turkeys (*Meleagris gallopavo*) reported some explicit form of censoring (Table A1.1). Censoring was also more often applied for species that were commonly captured using wire traps or rocket nets, and also for studies focused on newly hatched chicks, whereas species commonly captured using other methods, e.g., nighttime spotlighting, were less likely to be censored. These apparent differences may reflect researcher perception of the relative risk posed to birds by each capture method. Variable field practices among researchers, or different conditions among study systems, could result in a true difference in capture effects among studies, even for the same species observed using conventional methods. We therefore suggest that researchers use a systematic approach for detecting capture effects and mortality thresholds, which may ultimately be the best way to standardize results among studies and investigators.

In our case study of Ruffed Grouse, we found that mortality associated with capture persisted at least six days following release of the bird. The field methods we used for our study mirrored previous work on Ruffed Grouse (e.g., Devers et al. 2007, Skrip et al. 2011), and a six-day threshold aligns very closely with that used in Ruffed Grouse research (typically seven days; Small et al. 1991, Yoder et al. 2004, Devers et al. 2007, Skrip et al. 2011). The daily survival probabilities from our study suggest the mortality rate prior to day 7 ($1\text{-}S^6 = 0.117$) approximated the proportion of Ruffed Grouse that Small et al. (1991) reported dying during the first seven days postrelease (12.1% of 461 radio-marked Ruffed Grouse; Small et al. 1991). We also found that mortality during the first six days postrelease was reduced substantially during our second two field seasons compared to the first. Although this difference could be attributed to a number of environmental factors we did not measure, e.g., changes in predator density, it also coincided with changes to our field protocols designed to reduce stress and injury during capture. Schumacher (2002) similarly suggested that checking traps twice each day reduced rates of self-inflicted injury for Ruffed Grouse in North Carolina, but also noted a trade-off between more frequent trap checks and the total number of traps that could be monitored (and thus total capture success). We suggest that investigators adopt bidaily trap checks, and add concealment to both the top and sides of trap bodies, as standard protocols when using lily-pad traps (Gullion 1965) to capture Ruffed Grouse. These modifications may also help to shorten censorship times, which would benefit researchers by allowing a larger number of birds to contribute data.

The method we used to detect postrelease thresholds of mortality is easily implemented and widely applicable to other studies of radio-marked birds, and a number of previous studies have used similar approaches. Holt et al. (2009) evaluated thresholds at 1, 2, 3, 7, 14, and 21 days for Northern Bobwhite, and found no evidence for time-effects on postrelease survival. Working with translocated Wild Turkeys, Kane et al. (2007) evaluated staggered entry at 7, 14, 21, and 28 day intervals, and chose seven days as the most appropriate threshold based largely on qualitative differences in the number of mortalities observed during each interval. Our approach builds on these earlier works by modeling all possible dates within one month postrelease, thus providing an assessment of postrelease mortality thresholds across a continuous time scale and allowing for a more precise determination of the optimal threshold value. This is important because of the inherent trade-off between positive and negative bias when left-censoring individuals from a survival history; being too conservative results in unnecessary censorship of individuals that died for reasons not related to capture (positive bias), whereas being too liberal risks including mortalities related to capture (negative bias). By choosing the best-supported threshold from among all possible dates, this trade-off should, in theory, be optimized. A similar approach was used by Mathews et al. (2016) when evaluating thresholds for translocation effects in Sharp-tailed Grouse (*Tympanuchus phasianellus*), although in this case the authors used time periods that were binned into 10-day intervals and that extended to 150 days postrelease. Because the authors' central research question was related to translocation, and not capture effects per se, their use of a longer history and coarser time intervals were justified. We acknowledge that evaluating all possible date thresholds results in a relatively large number of models. Researchers could limit the total number of model comparisons by first examining estimates from models that allow full daily variation in survival, and use those results to inform construction of a subset of models within a more restricted date range.

Future studies of avian survival based on radio telemetry would likely benefit from more consistent evaluation of short-term effects of capture effects on survival, but this may not be necessary in all cases. For example, death of radio-marked individuals shortly following capture may be rare for species with high intrinsic rates of survival or where capture methods are less invasive. In such cases accounting for capture effects on mortality may be unnecessary, although nonlethal effects of capture may also persist in these situations (e.g., Cattet et al. 2008). In situations where radio-marked individuals do die within the first few weeks following capture, a systematic approach to detecting shifts in mortality offers an empirically justified tool to identify thresholds for censorship. We suggest that researchers focus on relatively short intervals, e.g., 1 month, and fine resolution, e.g., daily, data to best match the temporal scale at which these processes likely operate. Use of an empirical approach allows researchers to better account for capture-related impacts to survival while also limiting unnecessary censorship of birds whose deaths were more likely to be independent of capture. Formally addressing capture effects as a side objective can also help to elucidate modifications to field methods that reduce stress and injury to captured birds, thus improving animal welfare (e.g., Grisham et al. 2015).

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1147

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Appendix 1. Summary of literature review on current practices for censoring capture-related mortalities in upland game birds.

Table A1.1. Sources and information obtained during literature review to document researcher strategies for addressing capture-related mortality following release of radio-marked upland game birds from 2006 to 2016.

Source	**Species**	**Method**†	**Censor Period (Days)**	**Prop. Censored**‡
Devers et al. 2007	*Bonasa umbellus*	Delayed history	7	-
Skrip et al. 2011	*Bonasa umbellus*	Arbitrary	7	-
Anthony and Willis 2009	*Centrocercus urophasianus*	Did not censor	-	-
Baxter et al. 2008	*Centrocercus urophasianus*	Did not censor	-	-
Beck et al. 2006	*Centrocercus urophasianus*	Did not censor	-	-
Blomberg et al. 2013b	*Centrocercus urophasianus*	Did not censor	-	-
Blomberg et al. 2013a	*Centrocercus urophasianus*	Did not censor	-	-
Blomberg et al. 2014	*Centrocercus urophasianus*	Did not censor	-	-
Caudill et al. 2014	*Centrocercus urophasianus*	Systematic	0	-
Dahlgren et al. 2010	*Centrocercus urophasianus*	Cause of death	-	-
Gibson et al. 2013	*Centrocercus urophasianus*	Did not censor	-	-
Gregg et al. 2007	*Centrocercus urophasianus*	Did not censor	-	-
Gregg and Crawford 2009	*Centrocercus urophasianus*	Cause of death	1	0.06
Guttery et al. 2013	*Centrocercus urophasianus*	Cause of death	-	-
Holloran et al. 2010	*Centrocercus urophasianus*	Did not censor	-	-
Moynahan et al. 2006	*Centrocercus urophasianus*	Arbitrary	4	-
Buckley et al. 2015	*Colinus virginianus*	Arbitrary	7	-
DeMaso et al. 2014	*Colinus virginianus*	Arbitrary	14	-
Holt et al. 2012	*Colinus virginianus*	Did not censor	-	-
Holt et al. 2009	*Colinus virginianus*	Systematic	0	-
Janke and Gates 2012	*Colinus virginianus*	Arbitrary	7	0.02
Janke et al. 2015	*Colinus virginianus*	Delayed history	7	-
Lohr et al. 2011	*Colinus virginianus*	Arbitrary	7	0.04
Palmer and Wellendorf 2007	*Colinus virginianus*	Did not censor	-	-
Peters et al. 2015	*Colinus virginianus*	Delayed history	7	0.06
Rolland et al. 2010	*Colinus virginianus*	Did not censor	-	-
Scott et al. 2013	*Colinus virginianus*	Arbitrary	14	-
Seckinger et al. 2008	*Colinus virginianus*	Did not censor	-	-
Sisson et al. 2006	*Colinus virginianus*	Arbitrary	7	0.02
Tanner et al. 2012	*Colinus virginianus*	Did not censor	-	-
Terhune et al. 2007	*Colinus virginianus*	Did not censor	-	-
Terhune et al. 2010	*Colinus virginianus*	Did not censor	-	-
Unger et al. 2012	*Colinus virginianus*	Did not censor	-	-
West et al. 2012	*Colinus virginianus*	Did not censor	-	-

Anich et al. 2013	*Faclipennis canadensis*	Did not censor	-	-
Sandercock et al. 2011	*Lagopus lagopus*	Did not censor	-	-
Bowker et al. 2007	*Lyrurus tetrix*	Arbitrary	14	0.15
Pekkola et al. 2014	*Lyrurus tetrix*	Did not censor	-	-
Collier et al. 2007	*Meleagris gallopavo*	Arbitrary	21	-
Collier et al. 2009	*Meleagris gallopavo*	Delayed history	-	-
Holdstock et al. 2006	*Meleagris gallopavo*	Arbitrary	14	0.15
Humberg et al. 2009	*Meleagris gallopavo*	Arbitrary	7	0.05
Kane et al. 2007	*Meleagris gallopavo*	Systematic	7	0.07
Stephenson et al. 2011	*Oreortyx pictus*	Did not censor	-	-
Troy et al. 2013	*Oreortyx pictus*	Delayed history	10	-
Venturato et al. 2009	*Phasianus colchicus*	Systematic	-	-
Augustine and Sandercock 2011	*Tympanuchus cupido*	Did not censor	-	-
Winder et al. 2014	*Tympanuchus cupido*	Arbitrary	7	-
Carrlson et al. 2014	*Tympanuchus pallidicinctus*	Did not censor	-	-
Grisham and Boal 2015	*Tympanuchus pallidicinctus*	Arbitrary	14	-
Grisham et al. 2015	*Tympanuchus pallidicinctus*	Delayed history	7	-
Hagen et al. 2006	*Tympanuchus pallidicinctus*	Did not censor	-	-
Hagen et al. 2007	*Tympanuchus pallidicinctus*	Arbitrary	14	0.03
Lyons et al. 2009	*Tympanuchus pallidicinctus*	Arbitrary	10	0.16
Pirius et al. 2013	*Tympanuchus pallidicinctus*	Did not censor	-	-
Pitman et al. 2006	*Tympanuchus pallidicinctus*	Cause of death	-	-
Pitman et al. 2006	*Tympanuchus pallidicinctus*	Arbitrary	5	-
Manzer and Hannon 2008	*Tympanuchus phasuanellus*	Cause of death	-	-
Manzer and Hannon 2008	*Tympanuchus phasuanellus*	Did not censor	-	-
Mathews et al. 2016	*Tympanuchus phasuanellus*	Systematic	-	-

† Arbitrary – birds that die prior to a specified date are removed from the sample, timing of censorship not analytically-informed; Cause of Death – individuals are censored from the history based on evidence that suggest capture- or transmitter-related death; Delayed history – all birds enter the survival history following a specified censoring period; Did not censor – No censoring was applied or it was not reported in the paper; Systematic – some form of analytical approach was used to determine the most appropriate censorship date

‡ The proportion of the total sample of marked birds that were reported as censored following release due to capture-related mortality.

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