Estimating Duration of Short-Term Acute Effects of Capture Handling and Radiomarking

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ABSTRACT Radiotelemetry is used extensively in zoographic studies of wildlife species, including northern bobwhite (*Colinus virginianus*). These studies assume that radiomarking does not affect survival of marked individuals. However, most researchers implicitly acknowledge that capture, handling, and radiomarking may have short-term deleterious effects on individuals and, therefore, include in analyses only animals that survive an adjustment period of arbitrary length (often 7 days) following capture and marking. Length of adjustment period is rarely empirically based and may potentially bias survival estimates. We outline an analytical approach to determine an appropriate adjustment period and illustrate this approach by examining effects of time-since-marking on survival of 410 northern bobwhite captured during winter from 1997 to 2001, in Mississippi, USA. We modeled daily survival rates using time-since-marking as a covariate in the nest-survival model of Program MARK. Although survival varied among and within years, we found no evidence to suggest that standard adjustment periods of 7–14 days were appropriate for our sample. If adjustment periods are used in radiotelemetry studies, those that are empirically based may be more appropriate than arbitrarily set periods. (JOURNAL OF WILDLIFE MANAGEMENT 73(6):989–995; 2009)

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Radiotelemetry is used extensively in zoographic studies in general and studies of northern bobwhite (*Colinus virginianus*) in particular. The use of radiotelemetry allows researchers to estimate demographic parameters such as survival, reproduction, and dispersal. Use of radiotelemetry techniques has become increasingly common in northern bobwhite studies during the past 30 years.

A primary assumption of radiotelemetry studies is that radiomarking does not affect the animal's behavior, survival, or reproductive success (White and Garrott 1990, Withey et al. 2001). Effects of radiomarking may be either chronic and enduring or acute and ephemeral. We define chronic effects as those that manifest themselves over a seasonal or annual cycle and may continue as long as the animal retains the radio package or longer. Acute effects are those that affect the animal's behavior, survival, or reproductive success during a brief period after initial capture, handling, marking, and release (hereafter, handling effects) but diminish over time postrelease. Previous studies have explored chronic effects of radiomarking on northern bobwhite (Osborne et al. 1997, Parry et al. 1997, Corteville 1998) and reported evidence interpreted to both support (Guthery and Lusk 2004) and refute presence of chronic radio-effects (Folk et al. 2007, Palmer and Wellendorf 2007, Terhune et al. 2007). Chronic effects are clearly of concern because estimates of vital rates are biased if handling effects reduce fitness.

More typically, because most studies do not explicitly test radio-effects, researchers assume that chronic effects are negligible and parameter estimates from radiomarked birds are unbiased. However, researchers often attempt to address potential acute effects by excluding animals from the study during an initial period, implicitly acknowledging that handling effects may affect survival immediately after release. Pollock et al. (1989:11–12) suggested that bias associated with temporary handling effects "could be eliminated by having a conditioning period (e.g., 1 week) after tagging when an animal's survival time is not considered until it has survived that period."

Previous studies have used arbitrary adjustment periods ranging from 0 days to 14 days (Gilmer et al. 1974, Kurzejeski et al. 1987, Mueller et al. 1988, Burger et al. 1995, Osborne et al. 1997). However, even within the narrow domain of bobwhite literature, there is no consensus regarding the appropriate duration of adjustment periods and the manner in which exposure time of surviving individuals is handled. We reviewed 27 peer-reviewed publications reporting survival rates for wild adult northern bobwhite using radiotelemetry (Table 1). Of these publications, 14 reported using an exclusion period where data associated with northern bobwhite that died within the first 7 days postcapture were excluded from analysis, but all data collected from northern bobwhite that survived this period were included in the final analysis. Three publications used a similar exclusion protocol, except that the exclusion period was 14 days. Three publications reported using no adjustment period following capture and 3 publications made no reference to any type of

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Table 1. Peer-reviewed publications using adjustment periods for radiomarked northern bobwhite between 1993 and 2004 throughout the United States.

Adjustment period type	Source
7-day exclusion (include data for survivors beginning on day 1, exclude data for individuals that die within 7 days)	Robinette and Doerr 1993; Burger et al. 1995, 1998; Curtis et al. 1998; Pace et al. 1998; Taylor et al. 1999; Townsend et al. 1999; Sisson et al. 2000; Suchy and Munkel 2000; Taylor et al. 2000; Carter et al. 2002; Madison et al. 2002; Hernandez et al. 2003; Haines et al. 2004
14-day exclusion (include data for survivors beginning on day 1, exclude data for individuals that die within 14 days)	DeVos and Mueller 1993; DeVos and Speake 1995; Hernandez et al. 2005
No adjustment period	Mueller et al. 1993; Palmer and Wellendorf 2007; Terhune et al. 2007
No adjustment period reported	Dixon et al. 1996; Parry et al. 1997; Perez et al. 2002
14-day complete exclusion (all data from first 14 days excluded from analysis, regardless of fate of animal)	Williams et al. 2003, 2004
7-day complete exclusion (all data from first 7 days excluded from analysis, regardless of fate of animal)	Liu et al. 2000
14-day "conditioning" period[a]	Cox et al. 2004

[a] Authors report using this adjustment period type because it resulted in higher survival estimates and did not report how data were used for animals that died within first 14 days.

adjustment period. Two publications that appear to be the result of one study (Williams et al. 2003, 2004) reported using a 14-day adjustment period during which all data collected were excluded from analysis as suggested by Mueller at al. (1988) and Pollock et al. (1989). One publication (Liu et al. 2000) reported a 7-day adjustment period during which all data were excluded from analysis. Cox et al. (2004) examined effects of different adjustment periods on estimates of survival and concluded that using a 14-day adjustment period produced the greatest estimate of survival.

The presumption inherent in the use of any adjustment period is that for some brief period following capture, handling, and marking, birds experience an acute effect related to the marking process that declines over time, presumably to zero. Following this adjustment period, marked birds presumably exhibit similar behavior patterns and hazard functions as unmarked birds. The length of adjustment periods and the way in which they are applied will substantially affect survival estimates. If the adjustment period is too short, survival is underestimated because mortalities associated with marking and handling are included in the risk set. If the adjustment period is too long, survival will be overestimated because animals that died from causes unrelated to marking and handling are excluded from the risk set. Assuming that an adjustment period is necessary, researchers should provide an analytical justification for the selected period length. However, in none of the literature that we reviewed were analytical methods employed to empirically define the need for and appropriate duration of an adjustment period.

Our purpose was to describe an analytical framework for determining duration of possible handling effects on survival of radiomarked northern bobwhite and illustrate how a daily survival model with covariates defining time-since-capture, handling, and marking can be used within the nest-survival model of Program MARK to test competing hypotheses regarding duration of ephemeral acute effects.

STUDY AREA

We studied northern bobwhite on the Black Prairie Wildlife Management Area (BPWMA) in the Blackland prairie physiographic region of Mississippi, USA (88°33′W, 33°31′N; Pettry 1977). The BPWMA was approximately 2,300 ha, owned by the state of Mississippi, and managed by the Mississippi Department of Wildlife, Fisheries and Parks. Management of BPWMA was intended to demonstrate conservation practices in an agricultural setting. Habitat types on BPWMA were approximately 50% grass fields, 25% woods, and 25% agricultural fields. Woods were classified as areas of woody vegetation ≥ 2 m in height and $\geq 15\%$ continuous woody canopy cover. Agricultural fields were planted in a corn–soybean rotation and had 10-m field borders and 16-m-wide cover strips of herbaceous cover. Disturbance through prescribed fire, disking, and herbicide application was used on BPWMA to maintain early successional herbaceous communities.

METHODS

We captured northern bobwhite during a 68-day period beginning in early February of each year from 1997 to 2001. We captured birds in walk-in style wire traps (Stoddard 1931) baited with cracked corn. We checked traps twice daily, once in the morning after birds had foraged and returned to loafing cover and once in the evening after birds had foraged and returned to roost sites. After capture, we determined gender (M, F) and age (juv, ad) of each bird using standard procedures. We weighed each bird, banded it with a United States Geological Survey size 7 numbered aluminum leg band, fitted it with a 5–6-g necklace-style radiotransmitter (Advanced Telemetry Systems, Inc., Isanti, MN; American Wildlife Enterprises, Monticello, FL; Holohil Systems Ltd, Carp, ON, Canada), and released it at the capture site. Radiotransmitters had a 12-hour mortality sensor, a 20-cm antenna, and operated on a unique frequency between 148.000 MHz and 151.999 MHz. We held overnight in $60 \times 60 \times 30$-cm wooden boxes with cloth tops, birds caught during the evening trap-check when the temperature was $<10°$ C or when it was raining. We released birds held overnight the following morning at the capture site. We conducted capture, handling, and marking of northern bobwhite within the guidelines of The Ornithological Council (Gaunt and Oring 1999).

We monitored radiomarked bobwhite daily using a programmable receiver and a handheld 3-element Yagi antenna (Advanced Telemetry Systems, Inc.). We retrieved bird remains and collars immediately upon receiving a mortality signal. We assigned date of mortality as the median between 12 hours prior to the time that we first heard a mortality signal and the previous live signal.

We used survival-time information from radiomarked bobwhite to investigate duration of acute handling effects on their survival. We estimated daily survival during a 68-day period beginning in early February using the nest-survival model in Program MARK (Dinsmore et al. 2002). We used the nest-survival model because it handles unequal intervals between radiolocations and generates daily survival estimates in the presence of time-varying covariates necessary to examine acute handling effects. We assumed that capture, handling, and marking resulted in an acute effect on survival of radiomarked individuals of unknown duration. Moreover, we assumed that the magnitude of the acute effect diminished monotonically from time-since-marking.

We used a hierarchical model-selection procedure based on Akaike's Information Criterion (AIC; Akaike 1973) to identify the model that best characterized variation in survival between genders, among years, within years, and time-since-capture. In the first stage of this hierarchical model-selection process, we developed models to explain temporal variation in survival across and within years. At this stage, we developed competing models with no year effect [S(.)], a year effect [S(year)], a gender effect [S(gender)], gender and year effects [S(gender + year)], a within-year linear trend [S(within year t)], a year effect with a linear time trend within each year [S(year + within year t)], a linear time trend across years [S(across year T)], and a quadratic time trend across years [S(TT)]. Due to the time of year during which trapping occurred, we did not include any age-effect models because all northern bobwhite that we captured were of breeding age.

When we identified the best explanatory model for temporal variation in survival, we added covariates characterizing time-since-capture, handling, and marking. We constructed covariates to characterize a diminishing handling effect on survival of northern bobwhite that lasted an a priori hypothesized number of days. We constructed covariate models to test acute effects up to 21 days [S(best + 21 days)], 14 days [S(best + 14 days)], 7 days [S(best + 7 days)], 3 days [S(best + 3 days)], 2 days [S(best + 2 days)], and a 1-day effect [S(best + 1 day)]. We formatted the input file for Program MARK according to Dinsmore et al. (2002). We chose the 7- and 14-day periods because they are commonly used in radiotelemetry studies of northern bobwhite (Gilmer et al. 1974, Kurzejeski et al. 1987, Mueller et al. 1988, Burger et al. 1991, Osborne et al. 1997) and the 1-, 2-, 3-, and 21-day periods to bracket adjustment periods typically found in the literature.

Input files included 5 required pieces of information for each bird: the day since the beginning of the interval that the bird entered the risk set (i), the day that the bird was last known alive (j), the day the bird died (k), the fate of the bird (0 = censor, 1 = mortality), and frequency of that particular encounter history (Appendix). We scaled capture and mortality dates across all years so that the first day of the 68-day interval corresponded to the same Julian date regardless of year. Censoring occurred if a radiomarked bird survived past the end of the interval, emigrated from the study area, or experienced radio failure. If we censored the bird, time j = time k. We entered all birds as individual observations with unique encounter histories; thus, all frequencies were one. After we summarized the required information for each observation, we added 6 sets of 67 covariates to each observation. Each set of covariates corresponded to the explanatory models listed above for the length of the acute effect measured in days since capture, handling, and marking (l = 1 day, 2 days, 3 days, 7 days, 14 days, or 21 days). We coded covariates as zero until first day of capture, marking, and release of the bird. Then we assigned the length of the period of acute effect (l) to the first day of capture and counted down sequentially (Appendix) on each day following until the bird reached the maximum day of interest and then we assigned zeros as covariates for each following day of the interval. Covariates coded in this fashion characterized an acute handling effect that diminished linearly over the specified time interval (21 days, 14 days, 7 days, 3 days, 2 days, and 1 day) with no effect after the time interval. Coded in this fashion, we would interpret a negative beta parameter estimate for a handling effect of a given duration (l) as evidence for a linearly declining acute effect.

We illustrate effects on survival estimation of the 3 approaches reported in the bobwhite literature that we reviewed for handling adjustment periods (no adjustment, exclusion, and complete exclusion). The no-adjustment approach includes all data from all individuals immediately following capture. The exclusion approach is one under which data collected from animals that die within a specified adjustment period following capture are excluded but all data collected from survivors are included in the analysis. For the complete exclusion approach, all data collected during the adjustment period following capture are excluded from analysis regardless of fate.

We arbitrarily selected the 7- and 14-day adjustment periods in combination with each handling approach to illustrate the effect of selection of type and duration of adjustment period on survival estimates. We estimated seasonal survival (68 days beginning in early Feb) for each year from 1997 to 2001 for each of 5 combinations of adjustment technique and interval. The no-adjustment included all birds captured each season with data collection beginning the day of capture, marking, and release. We applied a 7- or 14-day interval to each of the exclusion and complete exclusion methods. For the 7- and 14-day exclusion method, we collected data on all birds beginning the first day of release and we excluded from survival analysis all data that we collected for birds that died within 7 days and 14 days, respectively. Likewise, we applied a 7- and 14-day interval to the complete exclusion method where we excluded from analyses all data collected for the first 7 days and 14 days, respectively, regardless of fate during the interval.

Table 2. Base models for survival estimates of radiomarked northern bobwhite on Black Prairie Wildlife Management Area, Mississippi, USA, for a 68-day period beginning 7 February, 1997–2001. Models were evaluated by sample-size-corrected Akaike's Information Criterion (AIC_c).

Model	AIC_c	ΔAIC_c	w_i[a]	K[b]	Deviance
S (year)	1,747.05	0.00	0.61	5	1,737.04
S (year + within year t)	1,748.30	1.25	0.32	6	1,736.29
S (TT)	1,752.56	5.51	0.04	3	1,746.55
S (across year T)	1,754.33	7.27	0.02	2	1,750.32
S (gender + year)	1,754.58	7.53	0.01	10	1,734.56
S (.)	1,806.85	59.80	0.00	1	1,804.84
S (within year t)	1,808.32	61.27	0.00	2	1,804.32
S (gender)	1,808.53	61.48	0.00	2	1,804.52

[a] Akaike wt.
[b] No. of parameters in each model.

RESULTS

During the 5-year study we captured and radiomarked 410 northern bobwhite. Seasonal totals were 80 in 1997 (36 F, 44 M), 102 in 1998 (54 F, 48 M), 97 in 1999 (39 F, 58 M), 88 in 2000 (39 F, 49 M), and 43 in 2001 (20 F, 23 M). Daily average number of radiomarked northern bobwhite in the risk set was 57 in 1997, 62 in 1998, 42 in 1999, 44 in 2000, and 18 in 2001. Sample size increased early during each 68-day season and remained constant through the remainder of the period. In general, sample sizes increased to the maximum level between days 10 and 24 and remained high through day 68.

Temporal variation in survival was best characterized by a model with year-specific survival (Akaike wt [w_i] = 0.61; Table 2). On 3 of the 5 year-effect beta parameter estimates 95% confidence intervals did not include zero (1997 = 1.641, SE = 0.311; 1998 = 1.554, SE = 0.297; 1999 = 0.241, SE = 0.243; 2000 = 0.255, SE = 0.241; 2001 = 3.772, SE = 0.194). A competing model included a linear time trend within years and year-specific survival ($\Delta AIC_c = 1.25$, $w_i = 0.32$). However, in this model, the 95% confidence interval on the beta parameter estimate for the linear time trend within a year overlapped zero ($\beta = -0.004$, SE = 0.005). Because there was no evidence for the linear time trend, we selected the year-specific model as the base model to express temporal variation in survival. When we added covariates characterizing handling effects to this model, 4 competing models had $\Delta AIC_c < 2$. Models characterizing acute handling effects with 14-, 21-, and 7-day duration had ΔAIC_c values of 0.38, 0.89, and 1.42, respectively. However, the best approximating model included only a year effect ($w_i = 0.338$; Table 3). All 95% confidence intervals of slope parameters characterizing handling effects included zero when we added them to the year-effect model (Table 3).

The use of different methods and time periods to correct for potential handling effects resulted in varying survival estimates over a 68-day period beginning on 7 February for the years 1997–2001. A 14-day exclusion period resulted in greater 68-day survival estimates each year. The 68-day survival estimates ranged from 0.73 (14-day complete exclusion) to 0.80 (14-day exclusion) in 1997, from 0.71 (14-day complete exclusion) to 0.80 (14-day exclusion) in 1998, from 0.26 (7-day complete exclusion) to 0.50 (14-day exclusion) in 1999, from 0.23 (14-day complete exclusion) to 0.41 (14-day exclusion) in 2000, and from 0.22 (no adjustment) to 0.48 (14-day exclusion) in 2001 (Table 4).

DISCUSSION

Contrary to the common 7-day adjustment period used in other northern bobwhite studies (Burger et al. 1994, 1998; Taylor et al. 1999; Sisson et al. 2000; Carter et al. 2002), we found no evidence to support a linearly declining acute handling effect of any duration on survival. Moreover, although the confidence intervals for handling effects of any duration included zero, the signs on the beta parameter estimates suggested declining survival with increasing time-since-capture. This counterintuitive observation is likely attributable to confounding of time-since-capture and seasonally varying survival. Daily survival declined marginally over the 68-day interval (Smith 2001, Szukaitis 2001), possibly associated with declining vegetative cover and phenology of raptor migrations (Holt 2003). We interpret the failure of time-since-marking covariates to contribute additional information to estimation of survival to mean there is no evidence for the hypothesis that there is a short-term, monotonically declining effect of marking on northern bobwhite daily survival. An alternative interpretation is that there is an effect, but it is of greater duration than those we tested (i.e., 1-, 2-, 3-, 7-, 14-, or 21-day; Abbott et al. 2005). However, in competing models that contained a time-since-marking effect, confidence intervals substantially overlapped zero and the sign of the coefficient was opposite to that predicted by the hypothesis.

Table 3. Acute radio-effects models for radiomarked northern bobwhite on Black Prairie Wildlife Management Area, Mississippi, USA, for a 68-day period beginning 7 February, 1997–2001. Models were evaluated by sample-size-corrected Akaike's Information Criterion (AIC_c).

Model	β[a]	SE[b]	AIC_c	ΔAIC_c	w_i[c]	K[d]	Deviance
S (year)			1,747.05	0.00	0.34	5	1,737.04
S (year + 14 days)	0.082	0.067	1,747.43	0.38	0.28	6	1,735.42
S (year + 21 days)	0.071	0.069	1,747.94	0.89	0.22	6	1,735.93
S (year + 7 days)	0.046	0.062	1,748.47	1.42	0.17	6	1,736.46
S (year + 3 days)	0.033	0.064	2,442.61	695.56	0.00	6	2,430.60
S (year + 2 days)	0.047	0.068	2,537.50	790.45	0.00	6	2,525.49
S (year + 1 day)	0.626	0.483	3,306.98	1,559.90	0.00	6	3,294.97

[a] Beta parameter estimate for handling effect of specified duration.
[b] SE for beta parameter estimate for handling effect of specified duration.
[c] Akaike wt.
[d] No. of parameters in each model.

Table 4. Survival (*S*) of radiomarked northern bobwhite on Black Prairie Wildlife Management Area, Mississippi, USA, for a 68-day period beginning 7 February, 1997–2001, estimated using 5 approaches for handling postcapture adjustment.

Adjustment type	Yr	n_F	n_M	n_{total}	*S*	SE
No adjustment	1997	36	44	80	0.742	0.054
	1998	54	48	102	0.723	0.052
	1999	39	58	97	0.305	0.052
	2000	39	49	88	0.308	0.051
	2001	20	23	43	0.218	0.064
	Total	188	222	410		
7-day exclusion[a]	1997	34	42	76	0.782	0.051
	1998	52	46	98	0.758	0.051
	1999	37	52	89	0.358	0.057
	2000	37	45	82	0.351	0.055
	2001	17	18	35	0.315	0.081
	Total	177	203	380		
7-day complete exclusion[b]	1997	32	39	71	0.753	0.057
	1998	52	46	98	0.717	0.058
	1999	37	51	88	0.264	0.054
	2000	36	44	80	0.276	0.053
	2001	17	18	35	0.255	0.078
	Total	174	198	372		
14-day exclusion[c]	1997	33	42	75	0.795	0.051
	1998	51	44	95	0.795	0.049
	1999	30	46	76	0.474	0.066
	2000	36	40	76	0.395	0.059
	2001	13	15	28	0.449	0.100
	Total	163	187	350		
14-day complete exclusion[d]	1997	31	38	69	0.734	0.063
	1998	51	44	95	0.711	0.065
	1999	30	44	74	0.284	0.066
	2000	34	39	73	0.234	0.054
	2001	13	15	28	0.337	0.102
	Total	159	180	339		

[a] Include data for survivors beginning on day 1, exclude data for individuals that die within 7 days.
[b] All data from first 7 days excluded from analysis, regardless of fate of animal.
[c] Include data for survivors beginning on day 1, exclude data for individuals that die within 14 days.
[d] All data from first 14 days excluded from analysis, regardless of fate of animal.

With regard to northern bobwhite, effects of radiomarking have been the subject of much discussion and debate (Guthery and Lusk 2004, 2007; Folk et al. 2007). Abbott et al. (2005) suggested that the mere act of handling birds caused effects that may last past 66 days for birds fitted with radiocollars and leg bands as well as birds fitted with leg bands only. Insofar as we did not have comparable survival estimates for unmarked northern bobwhite, we cannot make inferences to the overall effects of marking on northern bobwhite survival. Estimates of survival of radiomarked northern bobwhite might still be biased relative to unmarked birds. Our study merely addressed the common presumption that capture, handling, and marking results in some acute, ephemeral effect on survival that can be compensated for through use of an adjustment period. We tested this hypothesis using survival of birds that had been recently radiomarked versus those that had been marked for a greater duration of time. We conclude that if an acute, linearly declining effect does exist, it is small relative to the magnitude of within-year temporal variation.

Most researchers assume that the process of capture, handling, and marking may have a short-term effect on animal behavior and vulnerability to predation. To account for this handling effect, most studies report an adjustment period of arbitrary length during which survival and habitat use data are not used. However, application of this adjustment period is often inconsistent between studies. Of the peer-reviewed publications we reviewed, some authors excluded data only from northern bobwhite that died within the adjustment period whereas others excluded all data collected during the adjustment period regardless of fate of the animal (Table 1). Exclusion of only animals that died within an adjustment period will lead to overestimated survival rates because only animals that survive this period are included in the risk set for the adjustment period. Clearly, if an adjustment period is used, information from all animals regardless of fate should be excluded during this period.

The length of an adjustment period varies between studies but is typically an arbitrary length ranging from 1 day to 14 days (Gilmer et al. 1974, Kurzejeski et al. 1987, Mueller et al. 1988, Burger et al. 1991, Osborne et al. 1997). The implicit assumption is that effect of capture, handling, and marking is acute and maximized immediately following release and then declines monotonically to no effect over some short time interval. These acute effects are of unknown magnitude and duration. We observed little evidence of such temporally diminishing acute handling effects of radiomarked northern bobwhite survival. As such, we found little justification for use of an adjustment period after capture, handling, and marking to include radiomarked individuals in a risk set for survival analysis. Based on our results, the most unbiased estimate of survival of radiomarked northern bobwhite would be derived by including marked northern bobwhite in the risk set starting with the first live radiolocation after release.

MANAGEMENT IMPLICATIONS

Bro et al. (1999) suggested that researchers quantitatively assess handling effects on postrelease survival for each study using radiotelemetry. Our approach provides a repeatable, objective means to estimate existence, magnitude, and duration of acute handling effects. An assessment of duration and magnitude of an acute handling effect should be made to determine if an adjustment period is warranted. If an adjustment period is used, it should be a true adjustment period, or complete exclusion, where no data collected during the adjustment period are used in analysis regardless of the fate of an animal within the adjustment period.

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APPENDIX: INPUT FILE FORMAT

The following is an example Program MARK input file to examine effects of 1 day, 2 days, and 3 days since capture, handling, and marking on survival for a hypothetical 5-day interval from 1 February until 5 February, 1999 and 2000. The input file would be structured as shown in Table A1.

Nest survival group 1 are female birds captured in 1999, nest survival group 2 are male birds captured in 1999, nest survival group 3 are female birds captured in 2000, and nest survival group 4 are male birds captured in 2000. Each encounter history is preceded by the capture history for each bird. Capture histories include band number, gender, age (juv [J] or ad [A]), mortality factor, capture date, and mortality date. Following this are the required pieces of information for Program MARK, which include time *i* (first day alive in the interval), time *j* (last live encounter), time *k* (date of mortality detection), fate, and frequency (freq) of that encounter history (always = 1). After the required pieces of information are 3 sets of 5 covariates. Each set of 5 covariates corresponds to a 3-day, 2-day, and 1-day effect of time-since-capture, handling, and marking during the hypothetical 5-day interval. The bird illustrated in the first record was captured on 1 January 1999 and was censored on 27 February 1999 because of radio failure. This bird was known alive the first day of the interval ($i = 1$), last known alive the last day of the interval ($j = 5$), and date of censoring also the last day of the interval ($k = 5$). The covariates for 3-day acute radio-effect are coded as 2, 1, 0, 0, 0 because on the first day of the interval the animal is in its second day since capture, handling, and marking. Under the 3-day effect, we hypothesize the effect is greatest (3) on the first day of marking, and declines linearly to zero by the fourth day after marking. The covariates for the 2-day effect are coded as 1 0 0 0 0. Record number 5 was captured and marked on the first day of the interval; thus, 3-day radio-effect covariates are coded as 3 2 1 0 0. Similarly, 2- and 1-day effect covariates are coded as 2 1 0 0 0, and 1 0 0 0 0, respectively. Record number 8 was captured on the third day of the interval and survived beyond the end of the interval. Covariates for the 3-, 2-, and 1-day radio-effects are coded as 0 0 3 2 1, 0 0 2 1 0, and 0 0 1 0 0, respectively. Record number 12 was captured late in the interval and survived past the end of the interval while still in the acute period for the 3-day radio-effect. As such, covariates are included until the end of the period. Accordingly, covariates for record 11 for the 3-, 2-, and 1-day radio-effects are coded as 0 0 0 3 2, 0 0 0 2 1, and 0 0 0 1 0, respectively.

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Table A1. Example of the input file used in Program MARK illustrating 12 birds with associated capture-history information, encounter history, fate, and covariates for 3-, 2-, and 1-day radio-effects during a hypothetical 5-day interval beginning on February 1.

						3-day effect					2-day effect					1-day effect				
						Interval day					Interval day					Interval day				
Animal identification information	***i***	***j***	***k***	**Fate**	**Freq**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Nest survival group = 1;																				
/* 01 F J censor 01/31/99 02/27/99 */	1	5	5	0	1	2	1	0	0	0	1	0	0	0	0	0	0	0	0	0
/* 02 F A mammal 01/31/99 03/12/99 */	1	5	5	0	1	2	1	0	0	0	1	0	0	0	0	0	0	0	0	0
/* 03 F A mammal 02/01/99 03/29/99 */	1	5	5	0	1	3	2	1	0	0	2	1	0	0	0	1	0	0	0	0
Nest survival group = 2;																				
/* 04 M A censor 02/01/99 02/04/99 */	1	4	4	0	1	3	2	1	0	0	2	1	0	0	0	1	0	0	0	0
/* 05 M J raptor 02/01/99 02/05/99 */	1	4	5	1	1	3	2	1	0	0	2	1	0	0	0	1	0	0	0	0
/* 06 M J censor 02/02/99 03/12/99 */	2	5	5	0	1	0	3	2	1	0	0	2	1	0	0	0	1	0	0	0
Nest survival group = 3;																				
/* 07 F A raptor 02/03/00 02/04/00 */	3	3	4	1	1	0	0	3	0	0	0	0	2	0	0	0	0	1	0	0
/* 08 F J mammal 02/03/00 04/17/00 */	3	5	5	0	1	0	0	3	2	1	0	0	2	1	0	0	0	1	0	0
/* 09 F A censor 02/03/00 02/05/00 */	3	5	5	0	1	0	0	3	2	1	0	0	2	1	0	0	0	1	0	0
Nest survival group = 4;																				
/* 10 M A raptor 02/02/00 03/18/00 */	2	5	5	0	1	0	3	2	1	0	0	2	1	0	0	0	1	0	0	0
/* 11 M A raptor 02/02/00 02/04/00 */	2	3	4	1	1	0	3	2	0	0	0	2	1	0	0	0	1	0	0	0
/* 12 M J mammal 02/04/00 04/19/00 */	4	5	5	0	1	0	0	0	3	2	0	0	0	2	1	0	0	0	1	0