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Author(s): Kenneth H. Pollock, Scott R. Winterstein, Michael J. Conroy
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Estimation and Analysis of Survival Distributions for Radio-Tagged Animals

Kenneth H. Pollock,[1] Scott R. Winterstein,[2] and Michael J. Conroy[3]

[1] Department of Statistics, North Carolina State University, Box 8203,
Raleigh, North Carolina 27695-8203, U.S.A.

[2] Department of Fisheries and Wildlife, Michigan State University,
East Lansing, Michigan 48824, U.S.A.

[3] Georgia Cooperative Fish and Wildlife Research Unit, U.S. Fish and Wildlife Service,
School of Forest Resources, University of Georgia,
Athens, Georgia 30602, U.S.A.

SUMMARY

We present results on the estimation of survival distributions for an important problem in animal ecology. The problem involves estimation of survival distributions using radio-tagged animals. It requires allowance for censored observations due to radio failure, emigration from the study area, and animals surviving past the end of the study period. We show that survival analysis techniques already used in medical and engineering studies may be applied to this problem. Emphasis is placed on the model assumptions and the need for further research. An example to illustrate the strengths and weaknesses of this approach is presented.

1. Introduction

Radiotelemetry is becoming an increasingly popular methodology for studying wild animal populations. An animal, captured by trap, dart gun, or some other method, is fitted with a small radio transmitter and released. From release, the animal's unique radio signal can be monitored until the animal dies or is censored (see below).

The most common application of radiotelemetry technology has been to the study of animal movements in relation to daily activity patterns, seasonal changes, habitat types, and interaction with other animals. Time series approaches will become very important to the thorough analyses of these data (see Dunn and Gipson, 1977; Pantula and Pollock, 1985).

Biologists have also begun to use radio-tagged animals to study survival. Present techniques for analyzing the data from these studies assume that each survival event (typically an animal surviving a day) is independent and has a constant probability over all animals and all periods (see Trent and Rongstad, 1974; Bart and Robson, 1982). These assumptions are often believed to be unrealistic and restrictive. White (1983) has generalized their discrete approaches in the framework of band-return models (Brownie et al., 1985).

Typically an animal's exact survival time (at least to within 1 or 2 days) is known unless that survival time is right-censored. We suggest an approach based on the continuous survival models allowing right censoring that are widely used in medical and engineering applications (Kalbfleisch and Prentice, 1980; Cox and Oakes, 1984). We emphasize

Key words: Cox regression model; Exponential distribution; Kaplan–Meier estimates; Left truncation; Radiotelemetry; Right censoring; Survival analysis.

important assumptions of these models in the radiotelemetry framework and also present a numerical example. A shorter version of our approach appeared in Pollock (1984).

2. The Model

2.1 *Model Structure*

We assume that a random sample of n animals has been radio-tagged. Further, all animals are monitored regularly (usually daily) so that for practical purposes exact times of death are known. We also assume that there is a fixed study area to cover and if an animal with a functional radio is present it is found (with probability 1).

In terms of modelling we consider two sets of conceptual random variables:

(i) $T_1, T_2, \ldots, T_n$ form a set of survival times from tagging to death that would be observable if there were no censoring. We assume these constitute a random sample from some probability distribution with density $f(t; \boldsymbol{\theta})$ and survivor function $F(t; \boldsymbol{\theta}) = \Pr(T > t)$.

(ii) $C_1, C_2, \ldots, C_n$ form a set of censoring times that would be observable if there were no deaths. We assume these constitute a random sample from some probability distribution with density $g(c; \boldsymbol{\gamma})$ and survivor function $G(c; \boldsymbol{\gamma}) = \Pr(C > c)$.

The censoring could be due to any one of three possible causes:

(i) An animal has a transmitter that fails before the animal dies;
(ii) An animal emigrates out of the study area; and
(iii) An animal survives past the end of the study period.

In some studies it may be possible to ignore emigration for biological reasons.

2.2 *Likelihood Inference*

Assuming that one has a random censoring mechanism, which implies that $T_1, \ldots, T_n$ and $C_1, \ldots, C_n$ are independent, the likelihood for $\boldsymbol{\theta}$ (Kalbfleisch and Prentice, 1980, p. 40) is

$$L(\boldsymbol{\theta}) = \prod_{i=1}^{n} [f(t_i; \boldsymbol{\theta})]^{\delta_i}[F(c_i; \boldsymbol{\theta})]^{1-\delta_i}, \tag{1}$$

where δ_i is the censoring indicator. If $\delta_i = 1$, the observation is uncensored $(0 < t_i < c_i)$, while if $\delta_i = 0$ the observation is right-censored $(t_i > c_i)$. Note that it is also possible to write down a similar likelihood function for the censoring times $[L(\boldsymbol{\gamma})]$. If one assumes a parametric form for $f(t; \boldsymbol{\theta})$ (e.g., exponential distribution, Weibull distribution, gamma distribution), standard maximum likelihood inference could be carried out.

The Trent and Rongstad (1974) technique for analyzing data from radiotelemetry studies assumes that each survival event is independent and has constant probability. In the continuous framework we are adopting this is equivalent to using maximum likelihood inference assuming the exponential distribution.

2.3 *The Kaplan–Meier Procedure*

A nonparametric estimator was developed by Kaplan and Meier (1958) and is discussed in many books on survival analysis [see, for example, Cox and Oakes (1984, p. 48) or Kalbfleisch and Prentice (1980, p. 13) for details]. This estimator is also called the product limit estimator.

The survivor function $F(t)$ is the probability of an arbitrary animal in the population surviving t units of time from the beginning of the study. A nonparametric estimator of the survivor function can be obtained by restricting attention to the discrete time points when deaths occur, $a_1, a_2, \ldots, a_g$. We define $r_1, \ldots, r_g$ to be the numbers of animals at risk at these points, and $d_1, d_2, \ldots, d_g$ to be the numbers of deaths at the same points. The probability of surviving from 0 to a_1 is estimated by

$$\hat{F}(a_1) = 1 - d_1/r_1$$

because d_1/r_1 is the estimated proportion dying in that interval. The probability of surviving from a_1 to a_2 is similarly given by

$$1 - d_2/r_2,$$

and $\hat{F}(a_2)$ is then given by the product

$$\hat{F}(a_2) = (1 - d_1/r_1)(1 - d_2/r_2).$$

Therefore, the estimated survivor function for any arbitrary time t is given by

$$\hat{F}(t) = \prod_{j \mid a_j < t} (1 - d_j/r_j), \tag{2}$$

which is the mathematical way of stating that we are considering the product of all j terms for which a_j is less than the time t.

Cox and Oakes (1984, p. 51) also discuss how to estimate the variance of the estimate at an arbitrary time point using Greenwood's formula

$$\text{var}[\hat{F}(t)] = [\hat{F}(t)]^2 \sum_{j \mid a_j < t} \frac{d_j}{r_j(r_j - d_j)}, \tag{3}$$

where the summation is for all death times a_j less than t. They also present an alternative, simpler estimate that is better in the tails of the distribution:

$$\text{var}[\hat{F}(t)] = \frac{[\hat{F}(t)]^2[1 - \hat{F}(t)]}{r(t)}. \tag{4}$$

Approximate confidence intervals can be obtained using either of these equations. For example, a 95% confidence interval at $t = t_0$ would be

$$\hat{F}(t_0) \pm 1.96[\text{var } \hat{F}(t_0)]^{1/2} \tag{5}$$

because of the asymptotic (large-sample) normality of the estimates $\hat{F}(t)$.

2.4 *Hazard Function*

Another way of specifying the distribution of a continuous nonnegative random variable [besides the probability density $f(t)$ and the survivor function $F(t)$] is the hazard function (Cox and Oakes, 1984, p. 14; Kalbfleisch and Prentice, 1980, p. 6). The hazard function is the instantaneous rate of failure at $T = t$ conditional upon survival time t, and is defined mathematically as

$$h(t) = \lim_{\Delta t \to 0^+} \frac{\Pr(t \leqslant T \leqslant t + \Delta t \mid T \geqslant t)}{\Delta t}. \tag{6}$$

The hazard function is $h(t) = f(t)/F(t)$ from the definitions of $f(t)$ and $F(t)$. The distribution is exponential if and only if the hazard rate $h(t)$ is constant for all t.

2.5 *Proportional Hazards Model*

Sometimes the biologist may be interested in the influence of important covariates (such as weight at tagging) on the survival process. An important class of models here is the proportional hazards model (Cox, 1972; Cox and Oakes, 1984, p. 91). For this model the hazard function takes the form

$$h(t;\, \mathbf{z}) = h_0(t)\Psi(\mathbf{z}),$$

where $\mathbf{z}$ is a vector of covariates, $h_0(t)$ is the baseline hazard when $\mathbf{z} = \mathbf{0}$, and $\Psi(\mathbf{z})$ is a function where we require $\Psi(\mathbf{0}) = \mathbf{1}$ and typically

$$\Psi(\mathbf{z}) = \exp(\boldsymbol{\beta}^{\mathrm{T}}\mathbf{z}),$$

with $\boldsymbol{\beta}$ a vector of parameters analogous to regression parameters in a multiple regression problem.

As outlined by Cox and Oakes (1984), the reasons for considering this model are that (1) The effect of a "treatment" is to multiply the hazard by a constant factor and there is empirical evidence to support this approach; and (2) Censoring is easily accommodated and the technical problems of estimation are soluble when $h_0(t)$, the baseline hazard, is arbitrary.

3. Model Assumptions

Here we briefly discuss the assumptions of the model with the structure described in Section 2.1 as they apply to radiotelemetry data. As this is a new approach, further research on the validity of these assumptions in practice and on model robustness is required.

We have assumed that a random sample of animals of a particular age and sex class has been obtained. Consider, for example, a study on winter survival of mallards. If lighter adult males tend to be captured and they have lower survival rates, a negative bias to the survival estimates will result. Of course, this assumption is also crucial to survival estimates obtained from capture–recapture and band-return studies (Jolly, 1965; Seber, 1965; Pollock, 1981; Brownie et al., 1985).

This model requires the assumption that survival times are independent for the different animals. Again, this assumption is also required of capture–recapture and band-return models. Geese, which form tight family groups, would be an example where this assumption could fail. As another example, the death of a female animal, such as a black bear, still nursing her young would not be independent of the fate of those young.

In most studies time of death will be known to the nearest day. Therefore, the use of continuous-time survival distributions seems justified.

The assumption that the censoring mechanism is random is extremely important and requires more attention than can be given here. Possible violations could result from a predator killing an animal and also destroying the radio or an animal emigrating because it is more (or less) healthy than its companions. We wish to point out that medical studies often suffer a similar "emigration" problem; patients doing poorly (or well) may decide to leave the study.

One of the most important considerations in application of survival analysis to radiotelemetry data is the definition of a time origin. In some medical studies the natural time origin is time of treatment. In radiotelemetry there is no such natural time origin. In studies where all the animals are captured at or near the same time, the obvious time origin might be the date when the last animal was captured. It should be kept in mind that survival from the time origin could be vastly affected by seasonal effects so that, for example, survival for 1 month from a summer time origin could be quite different from survival for 1 month from a winter time origin. Seasonal effects are usually less important in medical studies.

In some studies, animals may be introduced into the study gradually over a long period of time. This could be due to practical problems of capturing animals all at one time or because the biologist deliberately wants to introduce more animals into the study to increase precision after a lot of animals have died. This is a situation where some animals will be subject to left truncation; they contribute to the likelihood only for times following their time of entry to the study. Cox and Oakes (1984, p. 178) discuss how the likelihood needs to be modified and they show how the Kaplan–Meier product limit estimator can be generalized to allow for left truncation.

4. Example

We examined data from the first year of a multiyear study on movements and overwintering survival of black ducks (*Anas rubripes*) conducted by the U.S. Fish and Wildlife Service under Conroy's direction. A detailed survival analysis of this study is presented in Conroy, Costanzo, and Stotts (1989); here we just present some analyses for illustration.

Fifty female black ducks from two locations in New Jersey were captured and fitted with radios. The ducks were captured over a period of about 4 weeks from 8 November 1983 to 14 December 1983 (Figure 1) and included 31 hatch-year birds (birds born during the previous breeding season) and 19 after-hatch-year birds (all birds at least 1 year of age). A condition index, body weight (g) divided by the wing length (mm), was calculated for each duck. The location and status (alive, missing, or dead) of each bird were recorded daily from the date of release until 15 February 1984, when the study was terminated. Diligent effort was made to locate each bird using roof-mounted antennas on trucks, strut-mounted antennas on fixed-wing aircraft, and hand-held antennas on foot and by boat. The pertinent data on each of the 50 radio-tagged ducks are presented in Figure 1 and Table 1.

Present techniques for analyzing data from radiotelemetry studies assume that each survival event is independent and has constant probability (Trent and Rongstad, 1974). Under this assumption in the continuous framework, the exponential survival distribution is obtained. Lee (1980) suggests testing for an underlying exponential by plotting the natural logarithm of the survival function [$\ln F(t)$] against the survival time; a linear trend is indicative of the exponential. We used the LIFETEST program (SAS, 1985) to calculate the Kaplan–Meier estimates listed in Table 1. We plotted $\ln[\hat{F}(t)]$ by time and the plot did not support use of the exponential distribution. Subsequent discussion will therefore be based primarily on the nonparametric Kaplan–Meier estimates.

Figure 2 is a plot of the Kaplan–Meier estimates listed in Table 1 and, for comparison, the curve obtained by fitting an exponential model. In obtaining these estimates, we limited the interval of interest to the 63-day period from 15 December 1983 to 15 February 1984. This is in accordance with our suggestion of possibly measuring survival time from the release of the last animal (Fig. 1). In this particular case, all birds were known to be alive on 15 December, radio transmitter battery life was projected to be approximately 90 days, and the period of interest (winter) was defined to be from mid-December until mid-February. Notice that after day 42 there is no recorded mortality and this is likely due to cessation of the hunting season on day 36 and also to the weather improving markedly after day 40. There was a total of 18 deaths, with 10 attributable to hunting and 8 due to natural causes. These results were consistent with the overall study (Conroy et al., 1988), where the probability of death due to hunting was approximately equal to the probability of death due to other causes. Causes of non-hunting mortality included predation (raccoons, red fox) and emaciation (winter stress).

As an example of a comparison of two survival distributions, we examined the null hypothesis that the survival distributions of hatch-year and after-hatch-year birds were identical. Plots of the estimated survival curves are given in Figure 3. Notice that the final

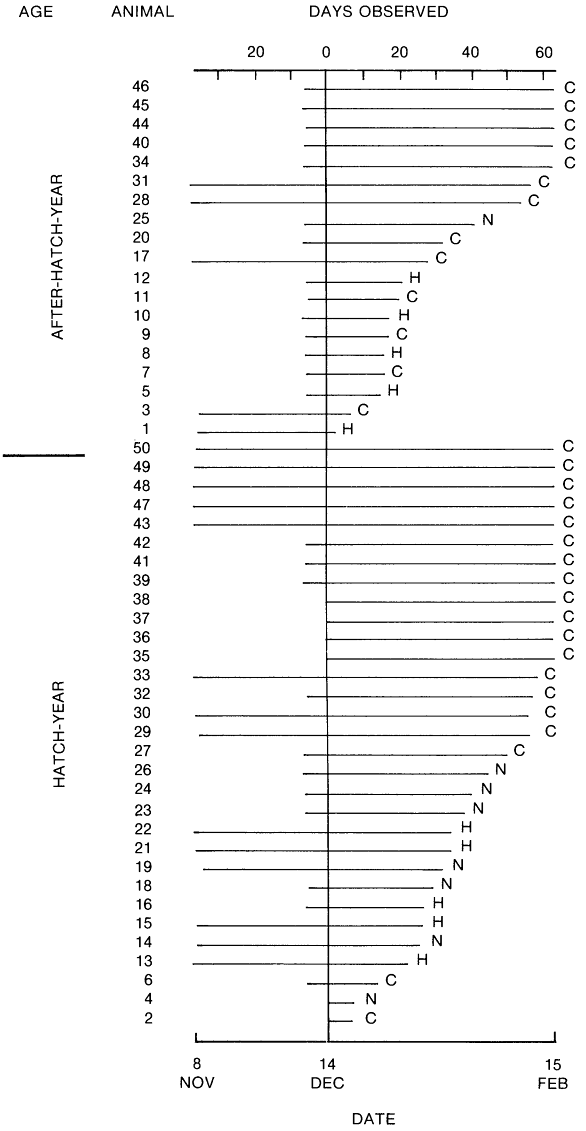

Figure 1. Observation histories for 50 female black ducks captured near New Jersey. Left endpoint of each line indicates the date the radio-tagged bird was released.

C: Censored; N: Death attributed to natural causes; H: Killed by hunter.

survival estimates are almost identical but that the survivor curves have quite different shapes, whereas in the overall study (Conroy et al., 1988) the hatch-year birds had a much lower overall survival rate of .60 versus .73 for the after-hatch-year birds, which is what the biologist would expect. Typically, young migratory birds do not fare well in their first winter and their first exposure to hunting.

First we fit the proportional hazards model using PHGLM (Harrell, 1983), which assumes that the hazard rates for the two age classes are proportional. Plots of the survival curves (Fig. 3) do not support this assumption, but for illustration, we fit the model

$$h_i(t) = h_0(t)e^{\beta(\text{age class})},$$

Table 1

Survival data and Kaplan–Meier estimates for female black ducks

Animal (i)	Survival[a] (t_i)	Indicator[b] (δ_i)	Age[c]	Weight (g)	Wing length (mm)	Condition[d] index	$\hat{F}(t_i)$[e]	Standard error
1	2	1	1	1,160	277	4.19	.9800	.0198
2	6	0	0	1,140	266	4.29	.9800	.0198
3	6	0	1	1,260	280	4.50	.9800	.0198
4	7	1	0	1,160	264	4.39	.9591	.0283
5	13	1	1	1,080	267	4.04	.9383	.0345
6	14	0	0	1,120	262	4.27	.9383	.0345
7	16	0	1	1,140	277	4.11	.9170	.0398
8	16	1	1	1,200	283	4.24	.9170	.0398
9	17	0	1	1,100	264	4.17	.8951	.0444
10	17	1	1	1,420	270	5.26	.8951	.0444
11	20	0	1	1,120	272	4.12	.8951	.0444
12	21	1	1	1,110	271	4.10	.8722	.0489
13	22	1	0	1,070	268	3.99	.8492	.0527
14	26	1	0	940	252	3.73	.8033	.0590
15	26	1	0	1,240	271	4.58	.8033	.0590
16	27	1	0	1,120	265	4.23	.7804	.0616
17	28	0	1	1,340	275	4.87	.7804	.0616
18	29	1	0	1,010	272	3.71	.7567	.0641
19	32	1	0	1,040	270	3.85	.7331	.0663
20	32	0	1	1,250	276	4.53	.7331	.0663
21	34	1	0	1,200	276	4.35	.6842	.0703
22	34	1	0	1,280	270	4.74	.6842	.0703
23	37	1	0	1,250	272	4.59	.6598	.0720
24	40	1	0	1,090	275	3.96	.6353	.0733
25	41	1	1	1,050	275	3.82	.6109	.0745
26	44	1	0	1,040	255	4.08	.5865	.0754
27	49	0	0	1,130	268	4.22	.5865	.0754
28	54	0	1	1,320	285	4.63	.5865	.0754
29	56	0	0	1,180	259	4.56	.5865	.0754
30	56	0	0	1,070	267	4.01	.5865	.0754
31	57	0	1	1,260	269	4.68	.5865	.0754
32	57	0	0	1,270	276	4.60	.5865	.0754
33	58	0	0	1,080	260	4.15	.5865	.0754
34	63	0	1	1,110	270	4.11	.5865	.0754
35	63	0	0	1,150	271	4.24	.5865	.0754
36	63	0	0	1,030	265	3.89	.5865	.0754
37	63	0	0	1,160	275	4.22	.5865	.0754
38	63	0	0	1,180	263	4.49	.5865	.0754
39	63	0	0	1,050	271	3.87	.5865	.0754
40	63	0	1	1,280	281	4.55	.5865	.0754
41	63	0	0	1,050	275	3.82	.5865	.0754
42	63	0	0	1,160	266	4.36	.5865	.0754
43	63	0	0	1,150	263	4.37	.5865	.0754
44	63	0	1	1,270	270	4.70	.5865	.0754
45	63	0	1	1,370	275	4.98	.5865	.0754
46	63	0	1	1,220	265	4.60	.5865	.0754
47	63	0	0	1,220	268	4.55	.5865	.0754
48	63	0	0	1,140	262	4.35	.5865	.0754
49	63	0	0	1,140	270	4.22	.5865	.0754
50	63	0	0	1,120	274	4.09	.5865	.0754

[a] Days observed.

[b] 0: Censored observation; 1: Observed death.

[c] 0: Hatch-year bird; 1: After-hatch-year bird.

[d] Weight (g)/Wing length (mm).

[e] Kaplan–Meier estimates.

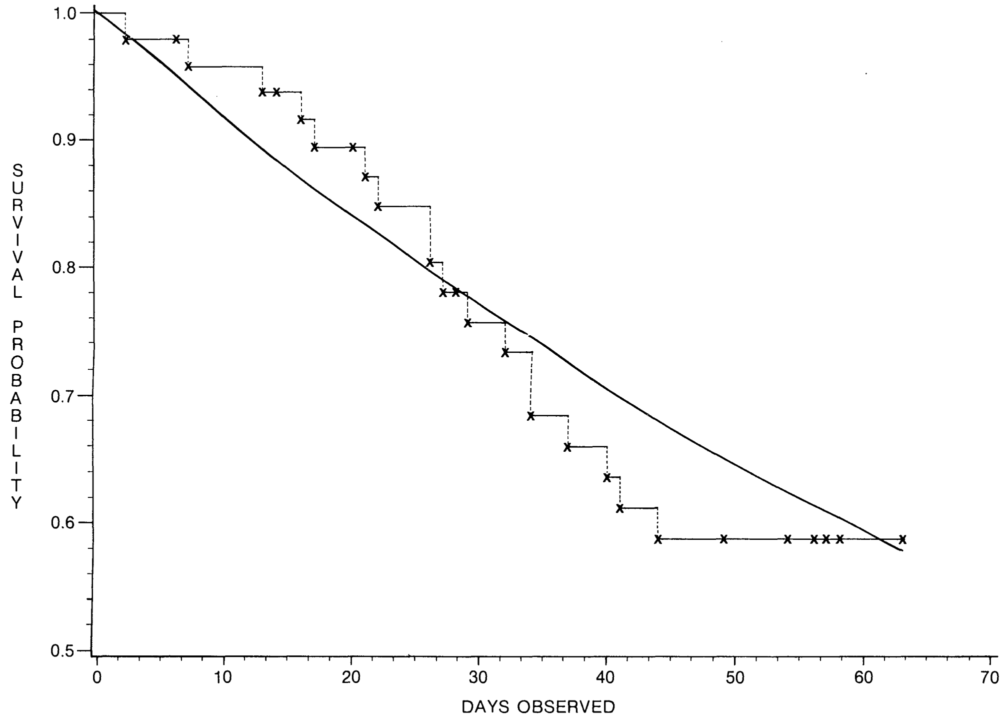

Figure 2. Survival distributions for female black ducks. x's are Kaplan–Meier estimates and are the values listed in Table 1. The solid curve represents the fit of the exponential equation:

$$\text{Survival probability} = e^{-.0087(\text{survival time})}.$$

where $h_i(t)$ is the hazard for the ith individual at time t, and $h_0(t)$ is the baseline hazard. The log-likelihood for a model containing no variables was −64.06. The log-likelihood for the age-class model [$\hat{\beta} = .14$, $\text{SE}(\hat{\beta}) = .50$] was −64.02. The value of twice the difference in the log-likelihoods approximates a χ_1^2 (see Cox and Oakes, 1984). Here, $\chi_1^2 = .08$ and there is no indication of a difference due to age.

Similar results were obtained when we tested for an age effect using generalized Wilcoxon and log-rank tests (see Kalbfleisch and Prentice, 1980) using program LIFETEST (SAS, 1985). The log-rank test is similar to the likelihood test discussed above in that it is optimal if the proportional hazards assumption is met. Neither the log-rank (test statistic = .5633, variance = 3.7668, $\chi_1^2 = .08$, $P = .98$) nor the generalized Wilcoxon (test statistic = −.8503, variance = 2.3706, $\chi_1^2 = .30$, $P = .78$) allowed us to reject the null hypothesis.

Breslow, Edler, and Berger (1984) present a new scores test for the null hypothesis of proportional hazards that is sensitive to the alternative of acceleration (hazard rates crossing). We obtained a significant asymptotic normal test result ($z = 3.12$, $P = .002$). This validates our suspicion from looking at Figure 3 that the two survival curves are not equal despite the lack of rejection of the likelihood ratio, log-rank, and generalized Wilcoxon tests, which do not work well when the hazards are not proportional.

As a final example, we examined the model

$$h_i(t) = h_0(t)e^{\beta(\text{condition index})}$$

for all 50 ducks and for each age class. Black duck ($n = 50$) survival was apparently related to condition index [log-likelihood for condition-index model = −61.685, log-likelihood for model with no covariates = −64.06, $\chi_1^2 = 4.75$, $P < .05$, $\hat{\beta} = 1.68$, $\text{SE}(\hat{\beta}) = .80$]. Given that

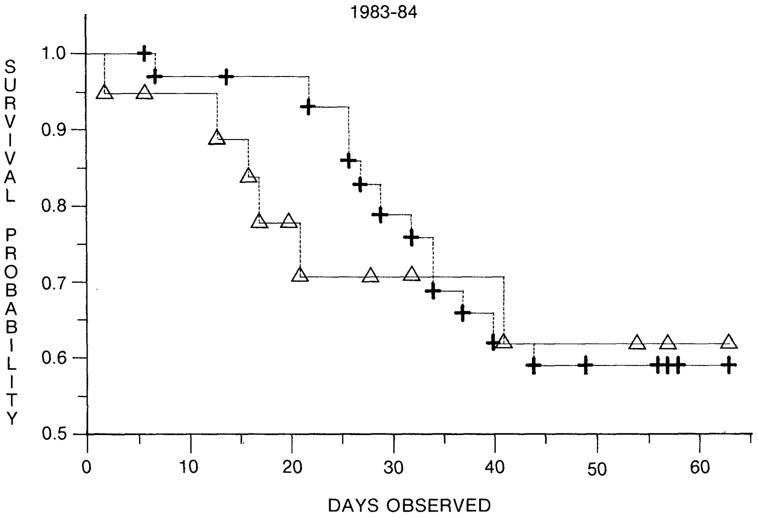

Figure 3. Survival distributions (Kaplan–Meier estimates) for hatch-year (+) and after-hatch-year (Δ) birds.

age apparently affects survival, we examined the effect of condition index within each age class. Survival of after-hatch-year birds ($n = 19$) was significantly related to condition index [log-likelihood for condition-index model = -13.21, log-likelihood for model with no covariates = -15.665, $\chi_1^2 = 4.91$, $P < .05$, $\hat{\beta} = 2.63$, $\mathrm{SE}(\hat{\beta}) = 1.37$]. Survival of hatch-year birds ($n = 31$) was, however, apparently not related to condition index (log-likelihood for condition-index model = -37.34, log-likelihood for model with no covariates = -37.87, $\chi_1^2 = 1.06$, $P > .25$, $\hat{\beta} = 1.14$, $\mathrm{SE}(\hat{\beta}) = 1.11$]. These results were consistent with those reported for the overall study by Conroy et al. (1988). We cannot explain biologically why the survival of hatch-year birds does not appear to be related to condition index. We would have expected condition index to be related to survival for both age classes of birds.

5. General Discussion

The radio-tagged survival analysis procedure presented above provides a general framework for analyses of these studies. Radiotelemetry is likely to become an even more common technique as the technology improves and costs are reduced. The large body of statistical research into survival analysis in medicine and engineering should prove valuable and the necessary computer packages already exist.

We believe that the techniques we have outlined, within the constraints of the listed assumptions, provide the researcher with a more realistic and sophisticated analysis than has heretofore been possible. While many biologists will be most interested in the distribution-free survival estimates themselves, most want the hypothesis testing and model fitting capabilities available. In particular, we believe the testing of ecological hypotheses regarding the influence of individual animal covariates (such as condition index) on survival using the proportional hazards model is extremely important.

In the analysis discussed in this paper we have put most emphasis on the Kaplan–Meier product limit estimator because of its simplicity and generality. An important question is: When should one use parametric modelling as opposed to nonparametric? Previous approaches to analysis of radiotelemetry data (Trent and Rongstad, 1974; Bart and Robson, 1982) could be viewed as very special cases of parametric modelling. Although discrete, their approaches are very similar to fitting an exponential distribution. Miller (1983) has compared maximum likelihood estimation and the Kaplan–Meier procedure when the underlying distribution is exponential and there is right censoring. As Miller points out, this comparison is biased against the Kaplan–Meier estimator and its efficiency can be low. This is especially troublesome when t is large and Miller states, "Parametric modelling should be considered as a means of increasing the precision in the estimation of small tail probabilities." He further states that it is surprising that so little work has been done on this question considering the importance of survival analysis in many disciplines (medicine, engineering).

In a review paper on right censoring and survival analysis, Lagakos (1979) discusses informative censoring (i.e., the censoring times are not independent of the survival times). Again, little work has been done on this problem. One practical approach is to calculate extreme bounds for the estimated survival curve by considering each censored observation to be either a death or a survivor until the end of the study. Of course, if there is a lot of censoring early in the study, these bounds can be very wide.

Finally, we emphasize the importance of definition of the time origin in this application of survival analysis. In our example the survival functions apply only to the black duck population between early winter (December 15) and early spring (February 15). Furthermore, the extension to left truncation with right censoring, which could be used if animals gradually enter the study, is very important, and will be studied further in another article (Pollock et al., 1989).

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RÉSUMÉ

Nous présentons des résultats sur l'estimation des distributions de survie pour un problème important en écologie animale. Le problème nécessite l'estimation de distributions de survie utilisant des animaux radio-marqués. On doit tolérer des observations censurées dues à un défaut de radio, à l'émigration à partir de la zone d'étude et à la survie d'animaux après la fin de la période d'étude. Nous montrons pour ce problème que l'on peut utiliser les techniques d'analyse de survie déjà utilisées dans les études médicales et industrielles. On insiste sur les suppositions du modèle et la nécessité de recherche ultérieure. On présente un exemple pour illustrer les points forts et les faiblesses de cette approche.

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