BAND RETURN MODELS: USE OF SOLICITED BANDS AND SEPARATION OF HUNTING AND NATURAL MORTALITY

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Abstract: The Brownie et al. (1985) band return models have been widely used to estimate survival and recovery rates for hunted species, especially migratory waterfowl. We developed a generalization of the Brownie models that allowed incorporation of solicited and reported bands into one analysis. This is an important addition to banding model literature, which has ignored solicited bands in the model formulation. Furthermore, if a reporting rate estimate is available from, for example, a reward banding study and a retrieval rate (1 − crippling loss rate) from a hunter questionnaire survey, we show that it is possible to estimate harvest rate, kill rate, and hence natural mortality rate in the presence of hunting. We illustrate our methodology on banding data for mallards (*Anas platyrhynchos*) banded in California from 1980 to 1983.

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Key words: *Anas platyrhynchos,* band return models, hunting mortality, mallards, natural mortality, reported tags, solicited tags.

Band recovery methodology has been widely used to estimate survival rates in multiyear banding studies of wildlife and fish populations (Youngs and Robson 1975, Brownie et al. 1985). The Brownie et al. (1985) methodology is often used but its formulation does not account for the fact that bands may be returned in two ways. Sometimes hunters are solicited by a wildlife management officer or scientist and asked if they shot any banded birds. Alternatively, a hunter may voluntarily report the band to the Bird Banding Laboratory (U.S. Fish and Wildl. Serv., Laurel, Md.) as is requested on the band. Because the Brownie et al. (1985) models only consider reported bands, Pollock et al. (1991) generalized their models to permit solicitation of tags in fish population studies. Here we show how to apply their generalized formulation, with some modification to allow for crippling losses, to wildlife banding studies. Furthermore, when band reporting rates are available from a reward banding study we show that it is possible to separately estimate hunting and natural mortality. This is important management information that was previously impossible to estimate with the other banding models.

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THE BROWNIE FORMULATION

Model Concepts

We use migratory birds to illustrate the methodology. A sample of migratory birds is captured, banded, and released into the population at roughly the same time each year for a number of successive years. The banded sample should represent the population of interest. The population is subjected to hunting each year, and hunters are requested to report bands from birds they have shot to the Bird Banding Laboratory. A bird alive at the start of the year has several possible fates (Brownie et al. 1985:14). Notation for the model includes the following: S = annual survival rate or probability of surviving from the banding period in year i to the banding period in year $i + 1$; K = annual kill rate or probability of being killed by a hunter during the year; γ = retrieval rate or probability that a killed bird is retrieved by the hunter; $H = \gamma K$ = annual harvest rate or probability of being harvested by a hunter during the year; and λ = band reporting rate or probability that a hunter will report a band from a harvested bird. These data only supply information about killed birds that are retrieved and whose bands are reported. Therefore, only the product $f = \lambda H = \lambda\gamma K$,

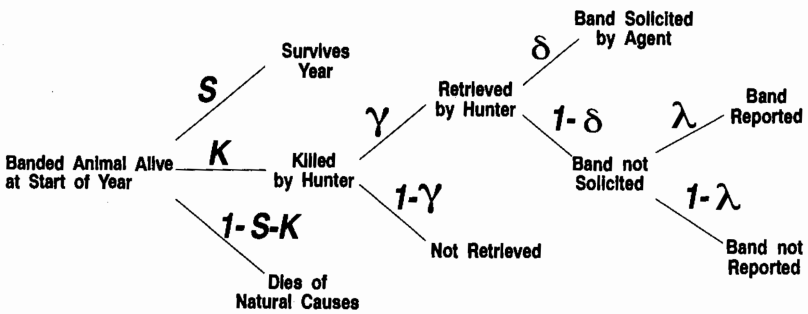

Fig. 1. Possible fates of a bird banded at the start of the year, extended from the diagrams in Brownie et al. (1985) to allow for solicitation.

which is called the band-recovery rate, is estimable, and the component rates λ, γ, and K are not separately estimable without additional information (Brownie et al. 1985:15).

Model Structure

Without stratifying animals by age class, Brownie et al. (1985) devised a set of 4 models for data of multiple years of banding and recoveries. The most general model is Model 0, for which S_i is the year-specific annual survival rate, f_i^* is the year-specific annual recovery rate for newly banded birds, and f_i is the year-specific annual recovery rate for previously banded birds.

Various restricted models can be specified by forcing certain parameters to remain constant over the years or over cohorts: Model 1 is a restriction of Model 0, where $f_i^* = f_i$ for all i. All banded birds have equal recovery rates in a given year irrespective of whether they are newly or previously banded. Model 2 is a restriction of Model 1 where $S_i = S$ for all years. All banded birds have constant annual survival rates over all years in the study. Model 3 is a restriction of Model 2 where $f_i = f$ for all years. All banded birds have constant annual survival and recovery rates over all study years.

These 4 models progress from general, Model 0, to restrictive, Model 3. It is possible to have more recovery than banding years and that not all survival and recovery rates are estimable for some models. Model 1 is probably most commonly useful, but on occasion the greater generality of Model 0 is necessary. Model 2 is sometimes used but it is rarely feasible to use the simplest model (Model 3). Brownie et al. (1985) also considered more general models for situations where age classes have differential survival and recovery rates. However, these models require that animals be of known age, which limits their use for many species.

Model Assumptions

There are 7 assumptions for multiyear banding models (Nichols et al. 1982, Pollock and Raveling 1982, Brownie et al. 1985, Pollock et al. 1991). Our general model, in the following section, was built on the same assumptions: (1) the banded sample represents the target population, (2) ages and sexes of banded birds are correctly determined, (3) there is no band loss, (4) survival rates are not influenced by the banding process, (5) the year (hunting season) of band recovery is correctly reported, (6) the fate of each banded bird is independent of the fates of all other banded birds, and (7) all banded birds within an identifiable class (age, sex) have the same annual survival and recovery rates.

GENERAL FORMULATION

The structure of the Brownie et al. (1985) models does not allow for bands to be solicited by survey agents or biologists, but a more useful structure for wildlife (and fisheries) studies can be developed (Fig. 1, modified from Pollock et al. 1991). There is a certain unknown probability (δ) that a band will be solicited. If we define the recovery rate of solicited bands as $f_s = H\delta = \gamma K\delta$ and the recovery rate of unsolicited bands as $f_r = H(1 - \delta)\lambda = \gamma K(1 - \delta)\lambda$, the quantities S, f_s, and f_r are estimable (Fig. 2). Estimation is now more complex because we have to consider 2 types of band recoveries (Table 1). We can obtain estimates for the above model and the generalizations of the other models in Brownie et al. (1985) using program SURVIV (White 1983). We used adult male mallard data from California for solicited and reported bands from 1980 to 1983 (Table 2).

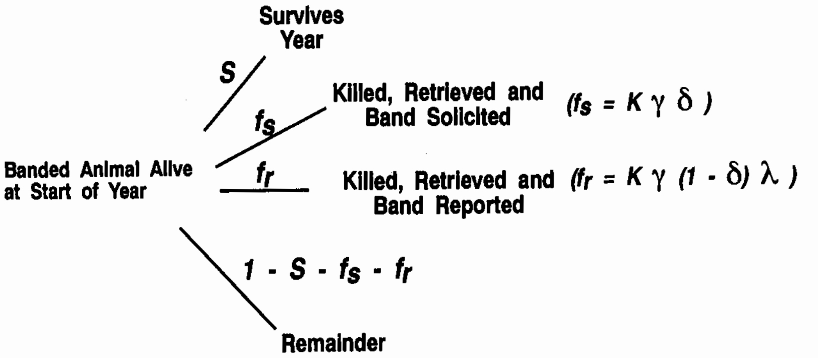

Fig. 2. Modified diagram for possible fates of a bird banded at the start of the year, from Brownie et al. (1985) extended to allow for solicitation.

Mallard Example

We used SURVIV to fit 8 models, and 5 models without constant solicited recovery rate fit the mallard data well (Table 3). On the basis of the least value of Akaike Information Criterion (Akaike 1971, 1974), the model that had constant survival rates and constant reported recovery rates performed better than the other models and had improved precision compared with the full model (Table 4). The expected values of cells for the best fitted model (Table 5) were similar to observed values (Table 2).

We estimated mallard survival rates where we used solicited and reported bands in a single analysis (Table 4). First we considered the full model and then the reduced model with constant survival and reported recovery rates over time. We analyzed data, using only reported bands and combining solicited and reported bands in one matrix. If we only used the reported bands the estimates were less efficient than the combined model (SE = 0.075 vs. SE = 0.062). If we used combined matrix of solicited and reported bands we found comparable precision (SE = 0.060 vs. SE = 0.062), but we could not estimate separate recovery rates for the 2 types of band returns. We emphasize that this was just one example. If there were few solicited bands then our model would not have gained much precision over the combined model.

SEPARATION OF HUNTING AND NATURAL MORTALITY

Harvest Rate (*H*)

We demonstrated that survival rate (S) and the 2 recovery rates (f_s, f_r) from a multiyear study could be estimated. In many studies, it is possible to estimate band reporting rate (λ) from a reward banding study (Henny and Burnham 1976, Nichols et al. 1991). From equation (1), we can estimate the harvest rate ($\hat{H}$) because we assume all solicited bands are reported.

$$\hat{H} = \hat{f}_s + \hat{f}_r/\hat{\lambda}. \tag{1}$$

Table 1. Expected numbers of band recoveries under the Model 0 generalization to allow for solicitation (Pollock et al. 1991). There are 3 banding years and 4 recovery years.

Yr banded	No. banded	Expected number of recoveries in year for solicited and reported bands				Mode of recovery[a]
		1	2	3	4	
1	N_1[b]	$N_1f^*_{1s}$[c]	$N_1S_1f_{2s}$[d]	$N_1S_1S_2f_{3s}$	$N_1S_1S_2S_3f_{4s}$	Solicited
		$N_1f^*_{1r}$	$N_1S_1f_{2r}$	$N_1S_1S_2f_{3r}$	$N_1S_1S_2S_3f_{4r}$	Reported
2	N_2		$N_2f^*_{2s}$	$N_2S_2f_{3s}$	$N_2S_2S_3f_{4s}$	Solicited
			$N_2f^*_{2r}$	$N_2S_2f_{3r}$	$N_2S_2S_3f_{4r}$	Reported
3	N_3			$N_3f^*_{3s}$	$N_3S_3f_{4s}$	Solicited
				$N_3f^*_{3r}$	$N_3S_3f_{4r}$	Reported

[a] Solicited from a wildlife agent or reported by a hunter.
[b] N_i is no. of birds banded in year i.
[c] f_{is} and f_{ir} are annual recovery rates for solicited (s) and reported (r) bands in year i.
[d] S_i is the annual survival rate in year i.

The approximate expected or mean value of $\hat{H}$ is

$$E(\hat{H}) \approx H\delta + \frac{H(1-\delta)\lambda}{\lambda}$$
$$= H\delta + H(1-\delta)$$
$$= H,$$

so that $\hat{H}$ will be unbiased in large samples. It is not necessary to estimate δ, because it cancels out in the derivation above.

Kill Rate (K)

If we estimate retrieval rate of birds shot by hunters (γ) by, for example, a hunter questionnaire survey (Martin and Carney 1977) then it is possible to estimate kill rate by

$$\hat{K} = \hat{H}/\hat{\gamma}. \tag{2}$$

Estimation of retrieval rate (1 − crippling loss rate) poses difficulties that we will discuss later.

Natural Mortality Rate (v)

We can estimate natural mortality that occurs in the presence of hunting mortality (i.e., expectation of natural death; Ricker 1975) by subtraction of the harvest rate from the total mortality rate $(1 - \hat{S})$ so that

$$\hat{v} = 1 - \hat{S} - \hat{K} \tag{3}$$

(in Appendix A we present approximate variances and covariances for these estimators). If

Table 2. Number of bandings and recoveries for a mallard study in California during 1980–83, with associated mode of recovery.

Yr banded	No. banded	Recovery year 1980	1981	1982	1983	Mode of recovery[a]
1980	1,471	26	17	7	5	Solicited
		80	56	29	16	Reported
1981	1,893		43	12	6	Solicited
			78	66	39	Reported
1982	1,076			7	11	Solicited
				66	31	Reported
1983	1,100				21	Solicited
					47	Reported

[a] Solicited from a wildlife agent or reported by a hunter.

Table 3. Log likelihood (LL), Akaike Information Criterion (AIC), and Chi-square goodness-of-fit test values under 8 submodels that allow for solicited and reported bands.[a] The submodels are identified by which variables are constrained to be constant. Data are from a mallard banding study in California from 1980 to 1983.

Model	No. of parameters	LL	AIC	χ^2	P-value
Full model	11	−55.842	133.684	11.649	0.2338
Constant S[b]	9	−55.899	129.797	11.764	0.3817
Constant f_s[c]	8	−63.272	142.544	25.954	0.0109
Constant f_r[d]	8	−56.863	129.725	13.543	0.3308
Constant S and f_s	6	−63.632	139.264	26.479	0.0225
Constant S and f_r[e]	6	−57.852	127.704	15.516	0.3438
Constant f_s and f_r	5	−65.128	140.257	29.236	0.0150
Constant S, f_s, and f_r	3	−65.494	136.989	29.913	0.0270

[a] Solicited from a wildlife agent or reported by a hunter.
[b] S: survival rate constant over years.
[c] f_s: solicited rate constant over years.
[d] f_r: reported rate constant over years.
[e] The best fitting model for the data.

Table 4. Estimated survival rates under different models and ways of analyzing banding data when both solicited and reported bands are possible.[a] Data are from a mallard banding study in California from 1980 to 1983.

	Survival rate in year					
	1980		1981		1982	
Model	$\hat{S}$	SE	$\hat{S}$	SE	$\hat{S}$	SE
Separate solicited and reported bands						
Full model	0.61	0.062	0.65	0.077	0.63	0.105
Constant S and f_r	0.63	0.030	0.63	0.030	0.63	0.030
Only reported bands						
Full model	0.64	0.075	0.63	0.084	0.73	0.14
Combined solicited and reported bands						
Full model	0.59	0.060	0.66	0.078	0.63	0.105

[a] Solicited from a wildlife agent or reported by a hunter.

Table 5. Expected number of band recoveries for mallard study in California under the generalized formulation with constant survival and reported recovery rates.

Yr banded	No. banded	Recovery year				Mode of recovery[a]
		1980	1981	1982	1983	
1980	1,471	26.03	21.17	5.53	5.53	Solicited
		77.99	48.78	30.51	19.08	Reported
1981	1,893		38.96	10.18	10.17	Solicited
			89.76	56.14	35.11	Reported
1982	1,076			10.34	10.34	Solicited
				57.05	35.68	Reported
1983	1,100				16.90	Solicited
					58.32	Reported

[a] Solicited from a wildlife agent or reported by a hunter.

Table 6. Estimated survival rate ($\hat{S}_i$), solicited[a] recovery rate ($\hat{f}_{is}$), reported[a] recovery rate ($\hat{f}_{ir}$), harvest rate ($\hat{H}_i$), kill rate ($\hat{K}_i$), and natural mortality ($\hat{v}_i$) for mallards banded in California during 1980–83.

Yr	Estimated rates					
	$\hat{S}_i$ (SE)	$\hat{f}_{is}$ (SE)	$\hat{f}_{ir}$ (SE)	$\hat{H}_i$ (SE)	$\hat{K}_i$ (SE)	$\hat{v}_i$ (SE)
1980	0.625 (0.029)	0.0177 (0.003)	0.053 (0.003)	0.133 (0.020)	0.158 (0.028)	0.216 (0.038)
1981	0.625 (0.029)	0.0230 (0.003)	0.053 (0.003)	0.138 (0.020)	0.165 (0.028)	0.210 (0.037)
1982	0.625 (0.029)	0.0096 (0.002)	0.053 (0.003)	0.125 (0.020)	0.149 (0.029)	0.226 (0.038)
1983		0.0154 (0.003)	0.053 (0.003)	0.131 (0.020)	0.155 (0.028)	

[a] Solicited from wildlife agent or reported by a hunter.

we make assumptions about the timing of the sources of mortality, it is possible to estimate other quantities (Ricker 1975). This was discussed in Pollock et al. (1991) but only for the case where the retrieval rate of dead animals was 1.

Mallard Example

We assumed the estimate of reporting rate and its standard error (J. D. Nichols, Patuxent Wildl. Res. Cent., pers. commun.), $\hat{\lambda} = 0.4601$ and $\text{SE}(\hat{\lambda}) = 0.0743$, obtained in 1988–89 for California applied over the earlier years we considered. We assumed $\hat{\gamma} = 0.84$ and $\text{SE}(\hat{\gamma}) = 0.0021$ from Martin and Carney (1977:31) using the mean retrieval rate for the Pacific Flyway ducks even though it is an old study. We then obtained estimates of $\hat{H}_i$, $\hat{K}_i$, and $\hat{v}_i$ with equations (1), (2), and (3) and their standard errors using equations in Appendix A (Table 6). Calculations are illustrated below:

$$\hat{H}_1 = \hat{f}_{1s} + \hat{f}_{1r}/\hat{\lambda} = 0.0177 + 0.0530/0.4601 = 0.1329,$$

$$\hat{K}_1 = \hat{H}_1/\hat{\gamma} = 0.1329/0.84 = 0.1582, \text{ and}$$

$$\hat{v}_1 = 1 - \hat{S}_1 - \hat{K}_1 = 1 - 0.6254 - 0.1582 = 0.2164.$$

DISCUSSION

For multiyear banding studies biologists usually collect data from solicited and reported bands. We have devised a coherent method of using all data in one comprehensive analysis that provides estimates of survival rate, solicited recovery rate, and reported recovery rate. We believe that this approach is an improvement over the original Brownie et al. (1985) formulation. If the only focus of analysis is survival estimation then the original Brownie et al. (1985) method will always give comparable precision to our approach if both types of recoveries are combined in one data matrix. To ignore data and use only reported recoveries is inappropriate, and the resulting estimates will always have lower precision with the degree of loss dependent on how many solicited bands are recovered.

A multiyear banding study combined with a reward banding study to estimate reporting rate and a special study to estimate retrieval rate (1 − crippling loss) enables wildlife biologists to estimate hunting and natural mortality rates (in the presence of hunting). We believe this is important to wildlife researchers and managers. Sound management of hunted species clearly requires knowledge of hunting and natural mortality components although historically good estimates of these quantities have not been available for most species.

There are some difficulties with estimation of hunting and natural mortality rates. Reward banding studies to estimate reporting rate (Henny and Burnham 1976, Nichols et al. 1991) are expensive so that estimates may not apply to the current population. Also estimates may be biased due to assumption violations. For example, not all reward bands may be reported. Hunter questionnaire surveys (Martin and Carney 1977) and other methods to estimate retrieval rates (1 − crippling loss rates) are also difficult to conduct and subject to potential biases. Future research in this area is clearly warranted due to the importance of separation of hunting and natural mortality for management purposes.

LITERATURE CITED

AKAIKE, H. 1971. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. C. Sahi, eds. Second international symposium on information theory. Akademia Krado, Budapest, Hungary.

———. 1974. A new look at the statistical model identification. Inst. Electr. and Electron. Eng. Trans. on Automat. Control. AC-19(6):716–723.

BROWNIE, C., D. R. ANDERSON, K. P. BURNHAM, AND D. S. ROBSON. 1985. Statistical inference from band recovery data: a handbook. Second ed. U.S. Fish and Wildl. Serv. Resour. Publ. 156. 305pp.

HENNY, C. J., AND K. P. BURNHAM. 1976. A reward band study of mallards to estimate band reporting rates. J. Wildl. Manage. 40:1–14.

MARTIN, E. M., AND S. M. CARNEY. 1977. Population ecology of the mallard: IV. A review of duck hunting regulations, activity and success, with special reference to the mallard. U.S. Fish and Wildl. Serv. Resour. Publ. 130. 137pp.

NICHOLS, J. D., R. J. BLOHM, R. E. REYNOLDS, J. E. TROST, J. E. HINES, AND J. P. BLADEN. 1991. Band reporting rates for mallards with reward bands of different dollar values. J. Wildl. Manage. 55:119–126.

———, S. L. STOKES, J. E. HINES, AND M. J. CONROY. 1982. Additional comments on the assumptions of homogeneous survival rates in modern bird banding estimation models. J. Wildl. Manage. 46: 953–962.

POLLOCK, K. H., J. M. HOENIG, AND C. M. JONES. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. Am. Fish. Soc. 12:423–434.

———, AND D. G. RAVELING. 1982. Assumptions of modern band-recovery models with emphasis on heterogeneous survival rates. J. Wildl. Manage. 46:88–98.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191. 382pp.

SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. Second ed. Macmillan, New York, N.Y. 654pp.

WHITE, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. J. Wildl. Manage. 47:716–728.

YOUNGS, W. D., AND D. S. ROBSON. 1975. Estimating survival rates from tag returns: model tests and sample size determinations. J. Fish. Res. Board Can. 32:2365–2371.

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APPENDIX A

Variances and Covariances of Hunting and Natural Mortality Estimators

Given that $\widehat{\text{var}}(\hat{S})$, $\widehat{\text{var}}(\hat{f}_s)$, $\widehat{\text{var}}(\hat{f}_r)$, $\widehat{\text{cov}}(\hat{S}, \hat{f}_s)$, $\widehat{\text{cov}}(\hat{S}, \hat{f}_r)$, and $\widehat{\text{cov}}(\hat{f}_s, \hat{f}_r)$ are available (e.g., from program SURVIV) and $\widehat{\text{var}}(\hat{\gamma})$ and $\widehat{\text{var}}(\hat{\lambda})$ are available from independent studies we have by the Taylor series method (Seber 1982:7)

$$\widehat{\text{var}}(\hat{H}) \simeq \widehat{\text{var}}(\hat{f}_s) + \left(\frac{\hat{f}_r}{\hat{\lambda}}\right)^2 \left[\frac{\widehat{\text{var}}(\hat{f}_r)}{\hat{f}_r^2} + \frac{\widehat{\text{var}}(\hat{\lambda})}{\hat{\lambda}^2}\right] + \frac{2}{\hat{\lambda}}\widehat{\text{cov}}(\hat{f}_s, \hat{f}_r), \quad \text{(A1)}$$

$$\widehat{\text{var}}(\hat{K}) \simeq (\hat{K})^2 \left[\frac{\widehat{\text{var}}(\hat{H})}{\hat{H}^2} + \frac{\widehat{\text{var}}(\hat{\gamma})}{\hat{\gamma}^2}\right], \quad \text{(A2)}$$

$$\widehat{\text{var}}(\hat{v}) \simeq \widehat{\text{var}}(\hat{S}) + \widehat{\text{var}}(\hat{K}) + 2\,\widehat{\text{cov}}(\hat{S}, \hat{K}), \quad \text{(A3)}$$

$$\widehat{\text{cov}}(\hat{S}, \hat{K}) \simeq \frac{1}{\hat{\gamma}}\widehat{\text{cov}}(\hat{S}, \hat{H}), \quad \text{(A4)}$$

$$\widehat{\text{cov}}(\hat{S}, \hat{H}) \simeq \widehat{\text{cov}}(\hat{S}, \hat{f}_s) + \frac{1}{\hat{\lambda}}\widehat{\text{cov}}(\hat{S}, \hat{f}_r), \quad \text{(A5)}$$

$$\widehat{\text{cov}}(\hat{K}, \hat{v}) \simeq -[\widehat{\text{cov}}(\hat{S}, \hat{K}) + \widehat{\text{var}}(\hat{K})], \quad \text{(A6)}$$

$$\widehat{\text{cov}}(\hat{S}, \hat{v}) \simeq -[\widehat{\text{cov}}(\hat{S}, \hat{K}) + \widehat{\text{var}}(\hat{S})], \quad \text{(A7)}$$

$$\widehat{\text{cov}}(\hat{H}, \hat{v}) \simeq -[\widehat{\text{cov}}(\hat{S}, \hat{H}) + \frac{1}{\hat{\gamma}}\widehat{\text{var}}(\hat{H})], \quad \text{(A8)}$$

and

$$\widehat{\text{cov}}(\hat{K}, \hat{H}) \simeq \frac{1}{\hat{\gamma}}\,\widehat{\text{var}}(\hat{H}). \quad \text{(A9)}$$