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The effect of lead exposure on survival of adult mallards in the Camargue, southern France

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Summary

1. In those countries where lead shot is still in use, a secondary effect of waterfowl hunting is lead poisoning from shot ingested by birds during bottom feeding. Moreover, waterfowl injured during hunting can die undetected as a direct or indirect consequence of wounds. The occurrence and influence of these types of lead exposure have often been estimated by the inspection of dead bodies, but this method will yield biased estimates if dead birds are not a random sample of the population.

2. We analysed a historical set of recoveries of adult mallard *Anas platyrynchos* ringed in the Camargue, southern France, over the period 1960–71, for which the amount and type of lead exposure had been determined by X-ray inspection before release. It was therefore possible to investigate the prevalence and effect of lead shot, avoiding the problem of post-stratification that may arise when only dead individuals are considered.

3. Among the captured birds, the proportion of gizzard-contaminated birds was constant (0·11) during the study period. In contrast, the proportion of birds carrying pellets in muscles increased linearly from 0·19 to 0·29. Males and females were similarly exposed to shot from both sources.

4. The relative survival of lead-affected mallards was 19% lower than unaffected birds for both types of lead exposure. The two sources of mortality were additive on a logarithmic scale and unaffected by sex.

5. Attempts to estimate the consequence of lead poisoning on population dynamics were not conclusive because of large confidence intervals in survival estimates. Moreover, it was still not clear how much mortality due to lead exposure should be considered as additive to other causes. We nevertheless advocate measures to control the long-term impact of lead exposure on waterfowl populations.

6. This work presents a new approach to the analysis of survival, in which the standard recovery models were reformulated in terms of monthly survival. This allows for the effect of a long ringing period during which mortality cannot be ignored. It also allows the estimation of parameters for newly marked birds without additional information. Since any within-year time interval can be considered, this approach can be used to investigate seasonal changes in mortality.

Key-words: crippling losses, injuries, in-season banding, lead poisoning, recoveries, ringing, seasonal survival.

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Introduction

Waterfowl hunting has several undesirable side-effects that might increase its impact on waterbird populations. In those countries where lead shot is still in use, as in most European countries, one of these is the dissemination of shot into waterfowl habitat. Birds having ingested these pellets may die of lead intoxication or lead poisoning (Bellrose 1959; Mudge 1983; Baldassarre & Bolen 1994). The impact of lead poisoning in natural populations of waterbirds was first quantified by Bellrose (1959), who estimated that between 1·6 and 2·4 million North American ducks, i.e. 2·5% of the autumn

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population, died from lead poisoning. Other studies have confirmed that lead poisoning has a dramatic effect on population dynamics (Birkhead & Perrins 1985; Pirot & Taris 1987; Hohman, Moore & Franson 1995; Grand *et al*. 1998). A second undesirable side-effect of hunting is crippling loss: these are birds killed but not retrieved or birds that die later from the injury they suffered (Pollock, Tsai & Hoenig 1994; Newton 1998). This type of mortality is not related as much to metal toxicity as it is to injuries caused by shots.

Evidence for the presence and amount of both types of lead exposure in wild populations is generally based on inspection of dead birds. However, a sample of dead birds may not be representative of the entire population, and the contamination rate is likely to be overestimated (Heitmeyer, Frederickson & Humburg 1993). Moreover, when the lead exposure rate is only known for dead birds, it is difficult to assess effect on population dynamics. An alternative approach is the analysis of capture–recapture or recovery data of birds for which lead exposure is known at the time of release. This avoids problems related to post-release stratification (i.e. when the exposure is assigned only after the death) and yields unbiased estimates of lead exposure mortality. Such a study could be done experimentally, by randomly exposing uncontaminated birds to a known amount of lead (Duranel 1999) or by inspecting the level of exposure through blood analysis (Grand *et al*. 1998) or X-ray photography (Madsen & Noer 1996). Although the experimental method would be preferable for investigating the toxic effects of lead, it would clearly not allow the study of injuries. Blood analysis of released birds was used recently by Grand *et al*. (1998) in a study of lead poisoning in female spectacled eider *Somateria fischeri*. These authors estimated that a lead concentration $\geq 0{\cdot}2$ p.p.m. in the blood caused a reduction of 0·34 in annual probability of survival, from 0·78 to 0·44. They suggested that such an increase in mortality could have led to the extinction of the local population. Madsen & Noer (1996), in a study of the impact of injuries on pink-footed geese *Anser brachyrhynchus*, estimated that birds carrying shotgun pellets in muscles (injured birds) had about 10% decreased survival compared with non-carriers. These studies demonstrate a negative effect of either type of lead pellet exposure, ingested or carried, on bird survival. However, these sources of mortality were studied independently and it is still unknown whether they act additively or interactively.

Here, we present a survival study based on recoveries of adult mallard *Anas platyrynchos* (L.) wintering in the Camargue (south of France), in which the type and amount of lead exposure was recorded by X-ray examination at the time of ringing. The Camargue system is one of the most important wintering areas in southern Europe for several species of waterbird (Isenmann 1993; Tamisier & Dehorter 1999) and has been included in the Ramsar Convention since 1986. Given the high persistence and slow settlement rate of lead pellets in marshes (Pain 1991; Flint 1998), traditional areas for waterfowl hunting, like the Camargue, are 'hot spots' for lead poisoning (Baldassarre & Bolen 1994). We investigated the influence of the two types of lead pellet exposure, the presence of ingested pellets (lead poisoning) and the presence of pellets in the muscles (injuries), on bird survival.

Materials and methods

PATTERN OF LEAD EXPOSURE

Mallards were captured from November to February for 12 consecutive years (1960–71) using baited traps. Before release, each bird was ringed, measured and X-rayed in order to count and locate lead pellets in its body. We assessed the proportion of exposed birds as the dependent variable in logistic models using year, month of release, sex and their interactions as explanatory variables. Models were fitted using GLIM software (Crawley 1993). The proportion of birds with ingested pellets (gizzard-contaminated birds) and those carrying pellets in the muscles (muscle-contaminated birds) were analysed separately. Note that double-contaminated mallards were included in both analyses. Model selection followed Akaike's information criterion (AIC) principle (Burnham & Anderson 1998). The model with the lowest AIC must be considered as the best compromise between the model deviance and the number of parameters in the model. Traditionally, parameter estimates should be derived by this retained model. Recently, Burnham & Anderson (1998) advocated the use of average estimates derived by a family of models, with AIC values within 3–7 points of the one of the retained model. Thus, model selection uncertainty was taken into account by averaging the estimates from those models within the arbitrary threshold of 4 points from the lowest AIC value (Burnham & Anderson 1998; Andreson & Burnam 1999).

SURVIVAL ANALYSIS

Model parameterization

The survival probability, S, could be estimated through maximum likelihood procedures from probabilistic models based on two quantities: the number of individuals released and the number of rings recovered (Brownie *et al*. 1985). The recovery of a ring corresponds to three distinct events: (i) the death of a marked individual; (ii) the retrieval of its body; and (iii) the return of the ring to the ringing organization. Each of these three events occurs with a specific probability (Brownie *et al*. 1985). The probabilities that correspond to (ii) and (iii) cannot be separated without additional information, for example from the use of ring rewards or solicited information (Nichols *et al.* 1991; Pollock, Tsai & Hoenig 1994), and only their product, denoted λ, is generally considered in recovery models (Seber

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Table 1. A recovery model considering the constant annual survival probability, S, as the product of two different survivals, S_h and S_b, related to the hunting, h, and the breeding, b, seasons, respectively. When a change in the relative importance of mortality causes is expected between the two seasons, different recovery rates should be considered (λ_h and λ_b in the table). Under the hypothesis that monthly survival, s_h and s_b, are constant during the respective seasons, over-season survival can be written as the product of monthly survival (e.g. $S_h = s_h^7$ if the hunting season lasts 7 months; see text for more details)

	Year of recovery					
	1		2		3	
Year of banding	h	b	h	b	h	b
1	$(1 - S_h)\lambda_h$	$S_h(1 - S_b)\lambda_b$	$S(1 - S_h)\lambda_h$	$SS_h(1 - S_b)\lambda_b$	$S^2(1 - S_h)\lambda_h$	$S^2S_h(1 - S_b)\lambda_b$
2			$(1 - S_h)\lambda_h$	$S_h(1 - S_b)\lambda_b$	$S(1 - S_h)\lambda_h$	$SS_h(1 - S_b)\lambda_b$
3					$(1 - S_h)\lambda_h$	$S_h(1 - S_b)\lambda_b$

1982; Anderson *et al.* 1985). However, a second parameterization of recovery models may arise when the probability of mortality is considered as being part of a general product, denoted f (Brownie *et al.* 1985). We will refer to these two parameterizations as the λ- and f-parameterization, respectively, with $f = (1 - S)\lambda$. Here, only the former has been used because of its flexibility in model construction (see below). Ring recovery rate λ is the recovery probability conditional on the animal's death. When different causes of mortality (i.e. hunting, starvation, predation) might lead to different retrieval or recovery probabilities, λ should be viewed as an 'average' recovery rate. Indeed $\lambda = \Sigma\alpha_j\lambda_j$, where α_j is the relative frequency of the cause of mortality j and λ_j is the recovery probability corresponding to that cause of mortality. A change in λ results from a change in the relative importance of a specific cause of mortality (α_j), from a change in the recovery propensities (λ_j) or both. Thus, for example, if survival during the hunting and the breeding seasons are estimated separately through a probabilistic model, a specific recovery rate must be considered for each period (Table 1) because changes in relative importance of mortality causes are expected. When birds are released on at least two or more occasions within the same year (e.g. in November and February), seasonal parameters (the model in Table 1) can be estimated (Tavecchia 2000).

Taking lead exposure into account

When lead exposure is measured from tissue or blood samples, lead contamination is generally treated as a continuous variable expressed as parts per million wet mass (p.p.m.) or grams per litre (usually μg dl^{-1}), respectively. Many authors agree on a concentration threshold under which lead intoxication is not critical, i.e. < 0·2 p.p.m. (Guitart *et al.* 1994; Pain 1992; Grand *et al.* 1998; Rocke, Brand & Mensik 1998; Samuel & Bowers 2000). However, when lead exposure is measured as the number of pellets ingested, it is difficult to relate exposure to such a contamination threshold. Indeed, the relationship between the number of ingested pellets and the subsequent lead concentration in blood or tissues is complicated by individual characteristics such as breeding stage, time of ingestion, diet and calcium levels (Guitart *et al.* 1994; Duranel 1999; Mezieres 1999). Bellrose (1959) found that one ingested lead shot had little effect on mortality. Similarly, Anderson, Havera & Zercher (2000), in order to compare recent and historical data on lead poisoning effects, considered > 2 ingested lead pellets as more critical for lead poisoning. To reduce the potential heterogeneity in survival among birds that had ingested lead pellets, we considered birds with only one pellet in the gizzard (n = 83) as uncontaminated birds. Additional studies confirmed that mortality of birds released with only one pellet in the gizzard was similar to that of uncontaminated birds (G. Tavecchia, unpublished data). The released mallards were thus categorized into four classes: (i) unexposed birds and birds with just one pellet in the gizzard; (ii) birds with > 1 pellet in the gizzard but no pellets elsewhere; (iii) birds with lead pellets in muscles or in other tissues but ≤ 1 pellet in the gizzard (injured birds); and (iv) birds with a double contamination (injured birds with more than one pellet in the gizzard). These four groups constitute a quasi-experimental factorial design, with the first factor 'lead in gizzard' (two levels), crossed with a second factor 'lead in muscles' (two levels).

Taking release date into account

Releases were spread over the hunting season. As a consequence, birds released early were exposed to a much higher risk of mortality during the first hunting season. To reduce this heterogeneity within each group of lead exposure, birds were sorted into four classes corresponding to the month of release (November, December, January and February). The differences in the number of days between the different months were judged negligible for this study. Such release-based groups allow the separate estimation of survival over the hunting season, denoted S_h (1 August–29 February), and over the breeding season, denoted S_b (1 March–31 July) (Table 1). In summary, a bird belonged to one of 32 groups based on combinations of sex (two levels), lead exposure (four levels) and time of release (four levels).

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Modelling mallard survival and improving parameter identifiability

In building recovery models, Anderson & Burnham (1999) advise careful choice of a limited number of effects beforehand that should relate to the biological questions of interest. First, we provided for a difference in recovery rate between the hunting period of the year of ringing (direct recovery rate, denoted λ'_h) and the recovery rate in subsequent years (indirect recovery rate, denoted λ_h) (Anderson *et al.* 1985; Brownie *et al.* 1985). We also considered a specific recovery rate for the summer recoveries, denoted λ_b (Table 1), expecting the incidence of hunting mortality to be lower than during the hunting season. Because the initial survival in any of the four release-based groups included a period shorter than 1 year, it was not directly comparable to yearly survival. This was unfortunate, because the initial recovery and survival rates, when specific, cannot be identified separately without additional information (Lakhani & Newton 1983; Anderson *et al.* 1985; Brownie *et al.* 1985; Freeman, Morgan & Catchpole 1992; Francis 1995; but see Morgan & Freeman 1989; Freeman & Morgan 1992). However, mallards in our study were released in different months of the same year, so we were able to overcome the identifiability problem by formulating the models in terms of monthly survival probabilities. We expressed survival over each time interval in the model as a product of the monthly survivals, s_h and s_b, during the hunting and the breeding season, respectively (note the lower case for monthly survivals). If survival is assumed to be constant within each season, the annual survival, S, for instance, is equal to the product $s_h^7\ s_b^5$ (Table 2). These relationships, which can be linearized by a log transformation, render all parameters identifiable. This can be verified by the method proposed in Catchpole & Morgan (1997) (see also Imbert 1998; Tavecchia 2000). This new approach considerably limits the number of parameters in the model: the number of group-specific survival parameters drops from 40 ($2 \times 4 \times 5$) in a model with unrelated initial survivals for each of the four release-based groups, to 16 ($2 \times 4 \times 2$).

Model notation and selection

A classical notation for recovery models is $S_{(x)}$, $\lambda_{(y)}$, where S is the survival parameter, λ is the ring recovery rate, and x and y are descriptors of the factors acting on S and λ. Also, x and y may interact. For instance, $S_{(s+t)}$, $\lambda_{(.)}$ depicts a model where survival varies with sex (denoted s) and time (denoted t) while λ is constant (notation '.'). The '+' between s and t means that the effects of sex and time are cumulative. With an interaction, the notation would be '$s \times t$' (Lebreton *et al.* 1992). In the present study, we have adapted the notation to accommodate the specific situation considered (two different monthly survival probabilities). First, 'S' always denotes survival over a period longer than a month (e.g. annual survival), while 's' always denotes the monthly survival. Additionally, the subscripts 'h' or 'b' signal the relevant season, hunting or breeding, respectively. When effects do not appear as index values, they apply to both monthly survivals in a similar way (additive effect). Models were fitted using MARK 1.9 (White & Burnham 1999). As for previous linear models, selection was based on AIC (Burnham & Anderson 1998). Model selection procedure began by assessing the fit of a simple model on pooled data (no lead- or period-of-release effects). Goodness-of-fit assessment was based on the bootstrap procedure in MARK 1.9 with 200 replications. The decrease in survival due to a specific type of lead exposure was expressed in relative terms as 1 – (annual survival of exposed birds/annual survival of not exposed birds).

Table 2. Survival to 31 July of birds belonging to the same exposure group and released at five different dates. s_h = monthly survival during hunting season (1 August–29 February), s_b = monthly survival during breeding season (1 March–31 July). Birds are treated as if released in the middle of the month

Birds released in:	
November	$s_h^{3\cdot5}\ s_b^5$
December	$s_h^{2\cdot5}\ s_b^5$
January	$s_h^{1\cdot5}\ s_b^5$
February	$s_h^{0\cdot5}\ s_b^5$
Previous years	$s_h^7\ s_b^5$

Results

LEAD EXPOSURE

Lead exposure patterns were analysed in 2740 adult mallards (1646 males and 1094 females) caught during winter between 1960 and 1971 (average number 228, range 27–817). The maximum count of pellets in the gizzard was 50, while exposure to a heavy load (> 9) of pellets in muscles was rare in our sample (Fig. 1). The initial model in both analyses assumed effects of time, month of release, sex and their second-order interaction. There was no significant extra binomial variation in the proportion of muscle-contaminated birds (Pearson's χ^2, $\chi^2_{28} = 30{\cdot}05$, $P = 0{\cdot}37$) but it was present in the gizzard-contaminated proportion ($\chi^2_{28} = 61{\cdot}68$, $P < 0{\cdot}01$). Consequently, in this second analysis, the deviance of subsequent models was divided by a scale factor of 2·2 (estimated as the model Pearson's χ^2 divided by its degrees of freedom). Subsequent AIC model values suggested that second-order interactions were not significant in either analysis (Table 3). From this point, the two analyses differed. The proportion of muscle-contaminated birds captured changed over time (Fig. 2), but neither month nor sex explained the incidence of muscle-contaminated birds that were captured. A trend over time was tested by treating the 'year' as a continuous variable. The lower AIC value (Table 3) of this model indicated that the proportion of muscle-contaminated birds increased linearly over time following the linear regression model:

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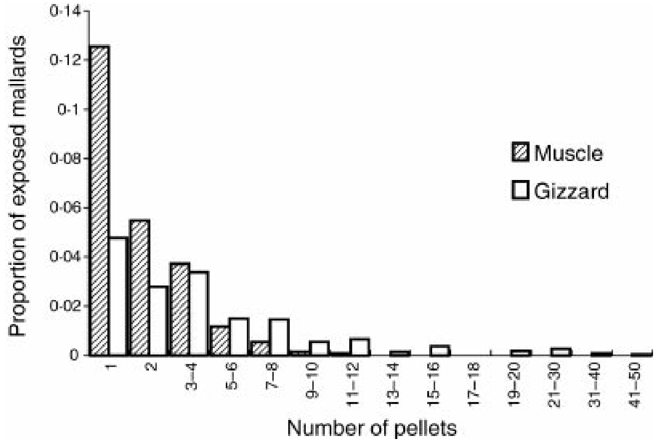

Fig. 1. Distribution of the prevalence of lead exposure in adult mallards according to number of pellets in their gizzard (white columns) or muscles (shaded columns) for the period 1960–71 (93 birds with double exposure are included in both series). For clarity 1872 animals without any pellets in their body (class 0) are not represented. Note that the last three classes span a wider interval.

Table 3. Logistic models for the analysis of the proportion of exposed birds. Gizzard and muscle contamination were treated separately (birds with a double contamination were considered in both analyses). In the analysis of the proportion of gizzard-contaminated birds a scale parameter (2·20) was used to correct for an extrabinomial variance. Notation: s = sex; m = month of release; yr = year as factor; Yr = year as continuous variable; ^ = interaction between two main effects. Upper case is for a continuous effect. Retained models (difference < 4 from the lowest AIC value) are in bold

Model	d.f.	Muscle-contaminated bird AIC	Gizzard-contaminated bird AIC
yr + *m* + *s* + yr ^ *m* + yr ^ *s* + *m* ^ *s*	28	−19·50	−39·28
yr + *m* + *s* + yr ^ *m* + yr ^ *s*	31	−25·12	−42·58
yr + *m* + *s* + *s.m* + yr ^ *s*	59	−39·04	−82·59
yr + *m* + *s* + yr ^ *m* + yr ^ *m*	39	−35·63	−58·05
yr + *m* + *s* + yr ^ *s*	62	−44·88	−84·71
yr + *m* + *s* + *m* ^ *s*	70	−55·27	−98·71
yr + *m* + *s*	73	−59·66	−100·93
yr + *m*	74	−57·30	−99·59
yr + *s*	76	−60·47	**−106·45**
m + *s*	84	−51·29	−102·94
yr	77	−59·07	**−105·26**
s	87	−48·58	**−108·26**
Yr	87	**−64·67**	−87·01
.	88	−47·50	−107·85

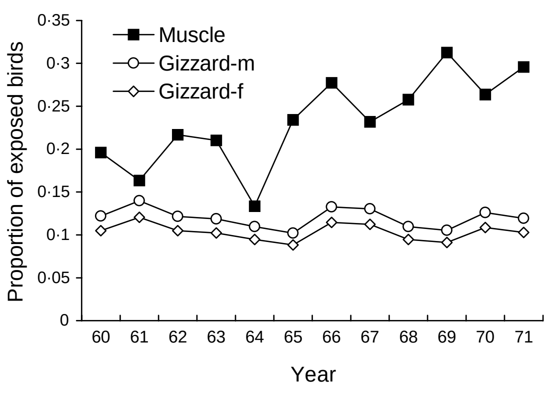

Fig. 2. Proportion of exposed birds according to the year and the type of exposure. For muscle-contaminated birds, estimates are from model M = yr. For gizzard-contaminated birds, estimates are derived by averaging those of models within 4 points from the lowest AIC (models in bold in Table 3). Muscle-contaminated birds = squares; gizzard-contaminated birds = circles (males) and diamonds (females).

$$\text{logit}(m) = -1{\cdot}71 + 0{\cdot}067(\text{yr}) \qquad \text{eqn 1}$$

where m = proportion of muscle-contaminated birds and yr = year.

In the analysis of gizzard-contaminated birds, females appeared less likely to be exposed than males. Indeed, the best model contained a sex effect (Table 4), but three other models were within four units of its AIC value: the constant model (.), the model with additive effect of years ($y + s$) and the model assuming yearly variation only (y). Year- and sex-specific estimates were thus obtained by the averaging technique (Fig. 2). However, the test of the sex effect (model 's' vs. model '.') was not significant ($F_{1,38} = 2{\cdot}39$, $P > 0{\cdot}5$). Finally the model assuming a trend over time in the proportion of gizzard-contaminated birds was rejected (Table 3). The estimated constant proportion of gizzard-contaminated birds in the sample was 0·11.

Table 4. Modelling recovery rate (λ'_h, λ_h and λ_b), and monthly survival probabilities during the hunting (s_h) and breeding seasons (s_b) according to sex (s) and lead exposure (G and M for pellets in gizzard and in muscles, respectively). For simplicity in model notation, the difference between breeding and hunting survival is noted as 'p' for 'period'. Except for model 1, birds are sorted into four classes based on the month of release (see text for details), and survival of newly and previously marked birds is expressed in terms of monthly survival (see Table 2). Retained models (AIC value within 4 points from the lowest value) are shown in bold

Number		Model	Deviance	np	AIC
1	$S(p)$	$\lambda'_{h(.)}\ \lambda_{h(.)}\lambda_{b(.)}$	3009·99	5	3019·99
2	$s_{(p)}$	$\lambda'_{h(.)}\ \lambda_{h(.)}\lambda_{b(.)}$	2985·05	5	2995·05
3	$s_{(t\times p)}$	$\lambda'_{h(.)}\ \lambda_{h(.)}\lambda_{b(.)}$	2970·87	16	3002·87
4	$s_{(p\times s)}$	$\lambda'_{h(\sigma)}\ \lambda_{h(\sigma)}\lambda_{b(\sigma)}$	2977·62	10	2997·62
5	$s_{(p\times s)}$	$\lambda'_h\lambda_h\lambda_b(G+M)$	2975·77	12	2999·77
6	$\boldsymbol{s_{(p\times s)}}$	$\boldsymbol{\lambda'_{h(.)}\ \lambda_{h(.)}\lambda_{b(s)}}$	**2978·42**	**8**	**2994·42**
7	$\boldsymbol{s(G\times M+s\times p)}$	$\boldsymbol{\lambda'_{h(.)}\ \lambda_{h(.)}\lambda_{b(s)}}$	**2968·62**	**11**	**2990·62**
8	$\boldsymbol{s(G+M+s\times p)}$	$\boldsymbol{\lambda'_{h(.)}\ \lambda_{h(.)}\lambda_{b(s)}}$	**2969·89**	**10**	**2989·96**
9	$\boldsymbol{s(M+s\times p)}$	$\boldsymbol{\lambda'_{h(.)}\ \lambda_{h(.)}\lambda_{b(s)}}$	**2973·62**	**9**	**2991·62**
10	$\boldsymbol{s(G+s\times p)}$	$\boldsymbol{\lambda'_{h(.)}\ \lambda_{h(.)}\lambda_{b(s)}}$	**2974·58**	**9**	**2992·58**

np = number of parameters.

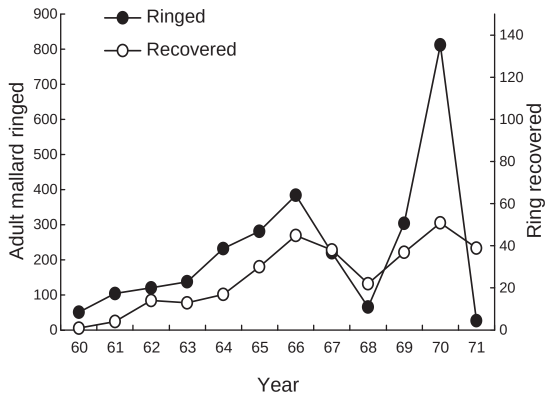

Fig. 3. Number of adult mallards ringed (black circles, principal axis) and recovered (white circles, secondary axis) over the study period.

LEAD EFFECTS ON SURVIVAL

The distribution of our sample among the four exposure groups was (i) 68% no exposure; (ii) 8% (219) gizzard-contaminated only; (iii) 20% (556) muscle-contaminated only; and (iv) 3·4% (93) both gizzard and muscle contaminated. Out of 2740 ringed mallards 311 were recovered (Fig. 3), 36 (11·6%) of which were during the breeding season. In general, releases were unequally spread from November to February (363 in November, 610 in December, 1542 in January and 225 in February). Model selection began by fitting a simple five-parameter model $S_{h(.)}S_{b(.)}\lambda'_{h(.)}\lambda_{h(.)}\lambda_{b(.)}$, assuming no time- or group-dependent parameters. Although crude this model provided a good description of the data set (goodness-of-fit test, $P = 0{\cdot}21$) and served as a basis for comparison with more refined models. We were not able to assess the fit of more general models assuming time and group effects because of problems of convergence in the bootstrap procedure. A model in which parameters of release-based groups were linked via monthly survival (model $s_{h(.)}s_{b(.)}\lambda'_{h(.)}\lambda_{h(.)}\lambda_{b(.)}$) had a lower AIC value (Table 4). A second reduction in AIC was obtained by considering a sex effect on monthly survival and recovery rate during the breeding season, but not the hunting season (model 6 in Table 4). This model yielded unreasonable parameter values ($\lambda > 1$) for the recovery rate during the summer (or survival > 1 when data were additionally analysed using the *f*-parameterization of Brownie *et al*. 1985). These unreasonable values probably resulted from the log-link function necessary to link the survival parameters. The model was not retained even when the recovery parameter was fixed. As a consequence of unreasonable values it was excluded for model averaging. A model assuming monthly survivals dependent on both types of lead exposure (G and M) had a better AIC value. In contrast, the model assuming a lead exposure effect on the recovery rate was not retained. Model $s(p\times s+G+M)\ \lambda'_{h(.)}\lambda_{h(.)}\lambda_{b(s)}$ was the one with the lowest AIC, but two other models had a similar AIC value. However, both assumed that survival was affected by both types of lead exposure (Table 4). Results of modelling lead effects on survival could be viewed in an ANOVA-like manner, in which deviance between the simpler model $s_{h(s)}s_{b(s)}$ or $s(s\times p)$ and the more general model $s(s\times P+G\times M)$ assuming lead exposure effects could be separated into three components (two main effects for the two types of lead exposure, G and M, and their interaction, $G^{\wedge}M$). Muscle contamination explained the largest part (49·0%) of the difference in deviance, the effect of gizzard-contamination explained an additional 38·1% (or 39·2% when tested alone) and the interaction explained the remaining 13·0%. Five models were within 4 points of AIC value (models 6–10 in Table 5). Parameter estimates were thus derived from the model averaging technique (Table 5; model 6 was excluded yielding unreasonable values for λ). The relative annual survival probability was about 8% lower for females than for males, mainly because of a difference in survival during the hunting season. Season did not affect male monthly survival in males, but female monthly survival was about 2% higher in the breeding

Table 5. Average estimates from models selected in Table 4 of recovery rate, hunting and summer season survival in relation to lead exposure (95% confidence interval for weighted average estimates in brackets). The relative monthly survival decrease due to lead in the gizzard (G) and injuries (M) is estimated as 19% for each effect. These two sources of mortality are additive on a logarithmic scale (hence multiplicative on the ordinary scale). Difference between male and female recovery rate during summer is not significant. The hunting season lasts from 1 August until the end of February and the breeding season from the 1 March until the 31 July

	Unexposed birds	Lead in gizzard (> 1)	Lead in muscles	Double exposure
S hunting				
Males	0·78 (0·66–0·86)	0·69 (0·52–0·82)	0·69 (0·54–0·81)	0·57 (0·36–0·76)
Females	0·72 (0·58–0·82)	0·64 (0·47–0·78)	0·64 (0·48–0·78)	0·53 (0·33–0·72)
S breeding				
Males	0·85 (0·69–0·94)	0·78 (0·59–0·90)	0·78 (0·64–0·88)	0·68 (0·56–0·84)
Females	0·85 (0·76–0·91)	0·79 (0·56–0·91)	0·79 (0·61–0·90)	0·68 (0·45–0·85)
Recovery rate				
λ'	0·374 (0·22–0·56)	0·374 (0·22–0·56)	0·374 (0·22–0·56)	0·374 (0·22–0·56)
λ hunting	0·181 (0·11–0·28)	0·181 (0·11–0·28)	0·181 (0·11–0·28)	0·181 (0·11–0·28)
λ breeding				
Males	0·049 (0·02–0·10)	0·049 (0·02–0·10)	0·049 (0·02–0·10)	0·049 (0·02–0·10)
Females	0·024 (0·01–0·07)	0·024 (0·01–0·07)	0·024 (0·01–0·07)	0·024 (0·01–0·07)

season than during the hunting season. Models with no period effect on survival were statistically acceptable. Although they were ruled out on biological grounds, they led to similar results. Recovery rates during the hunting season were 0·372 (0·228–0·542) for newly marked birds and 0·182 (0·117–0·272) for birds already marked. The recovery rate during the breeding season for males and females was 0·049 (0·024–0·097) and 0·024 (0·009–0·064), respectively. Due to the large uncertainty in the estimates, it was dubious whether there should be a sex difference in the recovery rate during the breeding season. However, because our main objective was to establish and assess the effect of lead exposure, we adopted the conservative point of view of maintaining separate recovery rate for the breeding season. Eventually, using values in Table 5, we estimated that the relative decrease in mortality due to lead exposure was 19% in both types. The two effects were additive on a logarithmic scale.

Discussion

STATISTICAL ASPECTS OF THE ANALYSIS

The present analysis, which shows that the presence of lead pellets in both the gizzard and muscles significantly reduce mallard survival, is based on recovery data for which lead exposure was measured at the time of ringing. Thus, it avoids the pitfall of post-stratification. The composition of the ringed sample might be biased if exposure alters the probability of being captured. This would in turn bias the estimated proportion of exposed birds, but not survival estimates. A possible bias in survival estimates originates from the fact that the level and type of lead exposure of a bird may have changed over time. Birds uncontaminated at the time of ringing may have been exposed to lead previously (Guitart *et al*. 1994) or subsequently; conversely, mallards exposed at the time of ringing may have expelled their pellets soon after release (Hovette 1972). These possible events are, however, conservative as regards the demonstration of lead exposure, making the negative effects more difficult to detect. Another potential problem is in determining the number of ingested pellets required to cause lead poisoning. In agreement with some previous studies, we considered two as the threshold (Bellrose 1959; Anderson, Havera & Zercher 2000). Parallel results (G. Tavecchia, unpublished data) showed that birds with only one ingested pellet have a survival probability similar to the one of unexposed birds, and in any case any effect would be conservative in detecting lead exposure effects.

One important assumption was that monthly survival could be considered constant over the hunting and breeding seasons. This is unlikely because survival varies through the year. However, the biggest changes are probably between the breeding and hunting seasons due to the breeding cycle and to changes in the hunting pressure. The variability within these periods is likely to be smaller than between them. In our analysis the goodness-of-fit of models based on two seasons supports this hypothesis. Moreover, annual survival rate (the product of over-season survivals) is consistent with previous findings of adult survival in mallards (Brownie *et al*. 1985; Nichols 1991; Smith & Reynolds 1992; Powell, Clark & Klaas 1995). This would not mean that survival *is* constant over the hunting and the breeding season, but that the bias we introduced in considering two periods only did not significantly affect the annual estimates. Bergan & Smith (1993) found that survival of adult female mallards over the period November to March was 0·78 (range 0·69–0·86). Our results across the groups are similar, while for unexposed birds they suggest a higher value (from August to March 0·72, range 0·58–0·82). This suggests that survival during August–September is more similar to the breeding period. On the other hand, in a study of spring–summer survival rate, Reynolds *et al.* (1995)

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found a survival probability of 0·57 (range 0·48–0·67) for adult females, which is consistent with that found in this study for exposed females only. These differences are not surprising considering that demographic parameters in mallards vary greatly between regions (Nichols, Williams & Caithness 1990; Powell, Clark & Klaas 1995) and the uncertainty in survival estimates.

To our knowledge this is the first study to consider simultaneously the effects of lead poisoning and injuries. The additivity of competing risks are better examined on the instantaneous mortality or hazard rate, –log S, as in human survival studies with respect to health (Elandt-Johnson & Johnson 1980). Thus, the log scale is appropriate for studying survival. In this way, we could demonstrate that the two types of exposure have additive effects, with lead poisoning affecting survival independently from pellets in the muscles. However, the use of the link function had some pitfalls that are discussed below.

A NEW MODEL FOR IN–SEASON RINGING

Another original feature of our analysis was the treatment of in-season ringing. When releases are spread over a long period, as is typical of in-season ringing, newly marked birds differ in their 'first-year' (initial) survival, for instance due to the month of release, because they have to survive unequal periods of time to the beginning of the next year. Because direct and indirect recovery rates are likely to be different (Anderson *et al.* 1985; Brownie *et al*. 1985), parameters for newly marked birds released within the same month are impossible to estimate separately without additional information (Lakhani & Newton 1983; Anderson *et al.* 1985; Brownie *et al.* 1985; Freeman, Morgan & Catchpole 1992; Francis 1995). The most common solution, used with true age-dependent models, consists of releasing birds with adult parameters in parallel. This was adopted by Thomson, Baillie & Peach (1999) to study post-fledging survival. Another possibility is to introduce additional constraints on parameters in the model by pooling some age classes (Catchpole, Freeman & Morgan 1995). Our solution was a mixture of both methods. We showed that the use of monthly survival made it possible to estimate all parameters under the unique assumption that monthly survival was constant over the chosen period; this yielded, at the same time, a more parsimonious model. In addition, the survival parameter for existing and newly marked birds could be rewritten using the common instantaneous survival. The modelling method presented here can be applied to estimate survival and recovery rates over any period within the year during which rings are recovered (Tavecchia 2000). An undesirable feature of our model is that the necessary log–link function might give, in some cases, unrealistic estimates (e.g. > 1). It allows consideration of survival of newly marked birds as a linear function of the period of release leading to a more parsimonious model. However, this function is not necessary for the recovery rate. A possible solution would be to use separate links for the two parameters. To our knowledge, this is the first study showing how parameters of newly marked animals can be estimated without additional information by taking advantage of releases spread over a long period.

LEAD EXPOSURE AND WINTERING POPULATIONS

Although injuries as well as lead poisoning appeared to be additive causes of mallard mortality, there was no effect of sex in the rate of exposure to lead pellets in the gizzard or muscles. This concords with other studies on mallards (Rocke, Brand & Mensik 1998; Mateo, Guitart & Green 2000) and other ducks (McCracken, Afton & Peters 2000; but see Pain 1990). Based on a 19% relative decrease in survival and on the proportion of gizzard-contaminated birds (> 1 pellet) in the data set, we estimate that 1·5% ($0{\cdot}19 \times 0{\cdot}08 \times 100$) of wintering mallards die of lead poisoning every year in the Camargue. The proportion of injured birds increased almost linearly from 19% in 1960 to 29% at the end of the study period. The number of hunters in the Camargue area over the period 1960–71 increased in a similar fashion (Tamisier & Dehorter 1999). According to our estimates, a substantial part (3·6–5·5%) of the wintering population is affected by mortality caused by injuries. We agree with Noer & Madsen (1996) that improved hunting efficiency is a management option for reducing crippling losses.

LEAD POISONING AND POPULATION CHANGE

Trends in the numbers of mallard over western Europe are not clear. In France, census data between 1950 and 1970 showed that the overall number of breeding birds was declining (Cramp & Simmons 1977). In the 1970s the species was considered in decline over most of its distribution (Cramp & Simmons 1977). Recent reviews reported a population decline in southern and eastern Europe (Romania, Spain and the Czech Republic) but an increase in the north and north-eastern areas (the Netherlands, Ukraine, Sweden and Great Britain; Flint & Krivenko 1990; Pirot & Fox 1990; Berndt & Hill in Hagemeijer & Blair 1997). Recent data from large census projects at the continental scale suggest a constant population. However, these data are difficult to interpret because of the thousands of hand-reared mallards introduced each year for hunting (Berndt & Hill in Hagemeijer & Blair 1997; Tamisier & Dehorter 1999). Theoretical and empirical studies suggest that lead poisoning might jeopardize population stability (Birkhead & Perrins 1985; Samuel 1992; Grand *et al.* 1998). To illustrate this point we estimated the growth rate, Λ, of two hypothetical populations with extreme values of lead-gizzard contamination (see the Appendix); the growth rate of a population where all females were exposed to lead poisoning might be reduced by 12%

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(see the Appendix), but in our case these results are not conclusive. Indeed, when considering the uncertainty in survival estimates, the ranges of possible values of Λ overlap. Samuel (1992) estimated that a 50% reduction in lead ingestion might produce an increase in the average annual population growth rate in mallard of 4·5%. These and our results are only indicative because mortality due to lead exposure has been considered additive to other sources. In contrast, Heitmeyer, Frederickson & Humburg (1993) showed that birds killed by hunters are three times more exposed to ingested lead pellets than birds sampled randomly from the same population, suggesting that lead exposure mortality is in part compensatory to hunting mortality.

A long-term management strategy for reducing lead poisoning effects is the use of non-toxic pellets (Baldassarre & Bolen 1994). Although such a policy is effective even in the short term (Anderson, Havera & Zercher 2000; Samuel & Bowers 2000), it has been adopted by few countries affected by waterfowl lead poisoning, especially in Europe. Whether lead shot should be substituted by a less toxic metal is currently under discussion in France. In the Camargue marshes, assuming a constant settlement rate, we estimated that the half-life of pellet availability to waterfowl (i.e. in the first 0–6 cm) is 46 years, and complete settlement will occur after 66 years only (lifetime expectancy of lead shots recalculated from values in Pain 1991). We therefore strongly advocate measures to control the long-term impact of lead exposure on waterfowl populations in southern Europe, in particular in 'hot-spot' areas like the Camargue (Pain 1990, 1991), in view of their importance in sustaining the wintering bird populations.

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Appendix

To illustrate the effect of lead poisoning mortality on the asymptotic population growth rate Λ (noted in uppercase to avoid confusion with the recovery rate), we built a two-age Leslie matrix model of two hypothetical populations with extreme values of lead gizzard contamination (100% and 0%). We maximized the population growth rate value by assuming (i) full reproduction at 1 year old; (ii) no breeding failure; (iii) no effect of lead contamination on reproduction performance; and (iv) that first-year birds are not lead contaminated. The matrix models were based on the following parameters.

Number of chicks per female	6·1	Bauer & Glutz von Blotzheim (1968)
Survival during brood-rearing	0·40	Hestbeck *et al.* (1989)
Survival to immature state	0·843	Hestbeck *et al.* (1989)
Immature female survival	0·532	Hestbeck *et al.* (1989); Nichols (1991)
Annual adult female survival (uncontaminated birds)	0·612	Present study
Annual adult female survival (gizzard-contaminated birds)	0·50	Present study

The confidence intervals for the survival parameters are estimated by the δ-technique (Seber 1982) using the variance–covariance values for the averaged estimates of Table 5. Given these parameters and the above assumptions, lead poisoning mortality causes a decrease in population growth rate of 12·6%. In our case, however, the uncertainty in the survival estimate prevents any definitive conclusion.

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