

Conservation breeding for reintroductions: assessing survival in a captive flock of houbara bustards

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Abstract

Conservation breeding for reintroduction is becoming a popular option for restoring threatened populations. Whereas post-release results are widely reported in the conservation literature, little empirical information is presented on the captive populations that often make such releases possible, even though fecundity, fertility and survival rates can have an impact on the outcome and cost of wild population re-establishment. We present results of survival analyses carried out on a captive population of houbara bustards to determine peak periods of mortality, and by identifying sources of variations in mortality to recognize the potential impact of management practices on productivity. There were two main mortality peaks: during incubation (53% survival of fertile eggs), and by 6 months post-hatching (75% survival of hatchlings). Management-related variables influencing survival of eggs and chicks included the year when laid, the cohort of females laying them, and possibly sex. Most post-hatching deaths were due to trauma and infectious diseases. Trauma-related deaths usually follow collisions with cages, and imply selection for the captive environment, an undesirable trend in populations maintained for reintroductions. Reducing losses during incubation would have the largest impact on production of birds for reintroduction, enabling the release of more birds, and reducing the overall costs of the project.

INTRODUCTION

The complementary efforts of captive breeding specialists and field conservationists towards restoring wildlife populations have been subsumed under the label of conservation breeding (Ebenhard, 1995). The reintroduction phase of conservation breeding programmes is the one most commonly reported in the literature, whereas the captive breeding phase is often neglected, despite having an important influence on the likelihood of population re-establishment.

Evaluations of programmes releasing both wild and captive-bred animals have shown that two parameters strongly influence the likelihood of population re-establishment: number of animals released, and quality of release-site habitat (Beck *et al.*, 1994; Wolf *et al.*, 1996; Green, 1997). When a captive population is the primary source of individuals for reintroduction, then the demographic characteristics of that population can dictate the rate at which individuals can be released, and thus the likelihood of post-release persistence.

Several arguments favour releasing as many individuals as possible. Releasing few animals may be counterproductive if the species is susceptible to inverse density-dependent fecundity, i.e., the Allee effect, in which case a minimum number of individuals should be released to ensure population establishment (Stephens & Sutherland, 1999). Releasing many animals provides an opportunity for systematic experimentation into alternative release techniques. Even large populations that willingly breed in captivity face genetic degeneration and domestication (Frankham *et al.*, 2000 and refs. therein). Reducing the number of generations of captive breeding needed to produce sufficient propagules would minimize the risk of such effects compromising the fitness of released animals, and lower the overall cost by reducing the time-span of the project.

Conservation breeding of houbara bustards (*Chlamydotis [undulata] macqueenii*) in Saudi Arabia has the explicit goal of re-establishing populations within secure protected areas. Houbara bustards can still be found in declining numbers throughout west and central Asia, and are seasonal visitors to Saudi Arabia. However, hunting and urban and agricultural development have virtually extirpated resident houbara in Saudi Arabia (Seddon & van Heezik, 1996). The captive

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founder flock, established within its former range at the National Wildlife Research Center, was collected as eggs and chicks in Pakistan between 1986 and 1988, and supplemented with individuals collected in the wild in Saudi Arabia, and from collections in Jordan. The policy for ensuring a growing captive population has been to retain at least 50 birds from each year's production for captive breeding, and to release the remainder. Consequently the number of birds released annually has varied widely (<20–100), according to demographic and environmental factors affecting captive productivity (Saint Jalme *et al.*, 1996).

We performed survival analyses on data from the captive houbara bustard flock, with the aim of identifying periods of high mortality, as well as factors that influence patterns of survival. The potential of management in contributing to these factors is discussed. Survival analysis has the advantage of providing an overview of the time frame and extent of mortality, as well as comparing survival between different groups of birds. We present these analyses as an example of the types of analyses that could be undertaken and reported for conservation breeding programmes for a variety of species.

METHODS

Data set

Since 1992, reproduction in the captive flock has been through artificial insemination, egg pulling to increase productivity, artificial incubation and hand-rearing (Saint Jalme & van Heezik, 1996). Dates of lay, of hatch and of death of almost all eggs, as well as identity of mothers, were recorded since 1992, as well as fathers of hatched chicks. Records were incomplete before this date. Causes of death were recorded when necropsies were performed, and were not known for eggs. Only eggs laid by inseminated females were included in the analyses. Eggs known to be infertile were excluded along with deaths occurring before incubation had begun. When egg losses occurred during the first 5 days of incubation staff could not confidently differentiate between losses due to infertility or to embryo death.

Precise dates of lay and hatch were unknown for founders. Their overall age was estimated from mean hatch dates for the flock: the lack of precision was considered to be negligible, since concerned individuals were at least 4 years old by 1992. The oldest birds in the flock were 17 years old at the end of 1999.

Survival analysis

We used Cox's regression model with the Kaplan–Meier (K–M) non-parametric estimator (SYSTAT V.9): the latter produces a life table and plot of the estimated survivor curve. The Cox regression model is a hybrid model – partly non-parametric in that it allows for an arbitrary survivor function like the K–M estimator, and partly parametric in that covariates are assumed to induce proportional shifts of the arbitrary hazard func-

tion. Parameters entered into the model as covariates when appropriate were sex, incubation treatment, mother's experience, cohort, and year of hatch. Identity of mother could not be entered as a covariate because the induced shifts in the hazard function were not proportional. The Cox model allows stratification, which is necessary in this case and also when comparing different groups of data. Stratification allows the survival pattern to vary markedly for cases with different values of the stratification variable while keeping the coefficients governing the hazard shifts common across all strata. The Tarone–Ware X^2 value was used in all cases unless otherwise specified.

Variables

The sex of dead birds was ascertained by necropsy, and in live birds by body size and plumage at the end of the first year of life. We compared survival of eggs laid in different years (1992–99), as well as survival until 6 months after hatching ('year laid').

We also compared survival of eggs and chicks laid by females from different cohorts ('cohort'). The 1982, 1989 and 1990 cohorts were excluded from the analysis, as in each cohort there were only two females contributing to the total number of eggs laid. Some very fecund females had contributed disproportionately to the total number of eggs in the early cohorts (1986 and 1988). Eggs laid by these females were culled from the data set using random numbers, until proportions were less unequal.

Survival of eggs from 25 mothers (each laying at least 14 eggs) and of chicks from 19 mothers (each hatching at least 14 chicks) was compared. Only eggs laid by experienced mothers were included in the analysis. Post-hatching survival of offspring from seven fathers was compared. The identity of fathers inseminating eggs was not recorded, so the effect of father on egg survival could not be determined.

Causes of death in the flock were grouped into eight categories: congenital abnormalities, human-related, impactions and perforations, neonatal, infectious diseases, metabolic disorders, traumas and other (e.g. drowning, stress, hepatic failure/steatosis, hyperthermia, hypothermia, thickening of gut wall, cloacal tumour). The primary cause of death was not always apparent. If there was significant doubt the record was defined as unknown. Ultimate origins of death are not always known, and can be multi-factorial. For example, infectious diseases may result from metabolic disorders, which could be of congenital origin; or deaths attributed to metabolic problems could have arisen as a result of nutritional deficiencies. Therefore causes of death are necessarily simplistic.

The importance of basing management practices on controlled, carefully designed trials is illustrated in the examination of the variable 'incubation treatment'. Since 1994, with the aim of improving hatchability, some eggs have been incubated under females for varying lengths of time (range = 1–22 days; 49% of eggs for 1–2 days,

33% for 3–6 days and 18% for >6 days). Simple comparisons of mean hatchability indicated higher survival of eggs incubated by females, and so this protocol was incorporated into incubation management, and applied to a proportion of eggs each year. Here we compare the survival of eggs naturally incubated for any length of time (PNI) with that of eggs incubated only artificially (AI), controlling for other variables potentially influencing survival. Data from the years 1996 to 1999 were used, by which time other incubation variables were more constant.

RESULTS

Survival during incubation

Mean incubation period was 23.5 days (SD = 0.9, range: 20–27, $n = 760$). Between 1992 and 1999 2917 eggs were laid: 45.8% of these hatched. Infertile eggs were laid by un-inseminated females (13.5%), and by inseminated females (6.8%). Some eggs broke or had soft shells (7.2%), and some died during incubation (26.6%). Survival analyses on all eggs laid between 1992 and 1999 indicated that 53% of fertile eggs had hatched (Fig. 1). However, uncertainty as to the cause of early losses (infertility and/or embryo death) meant that a precise figure for hatchability could not be calculated. If all losses before 5 days of age ($n = 400$) were in fact infertile eggs, then 23.7% of eggs laid by inseminated females were infertile, and hatchability rose to 69%.

Effect of incubation treatment and mothers

When no covariates were entered into the model, eggs incubated under females for any length of time (PNI) showed better survival than eggs incubated only artificially (AI) ($X^2 = 10.94$, $n = 553$ AI eggs; $n = 609$ PNI

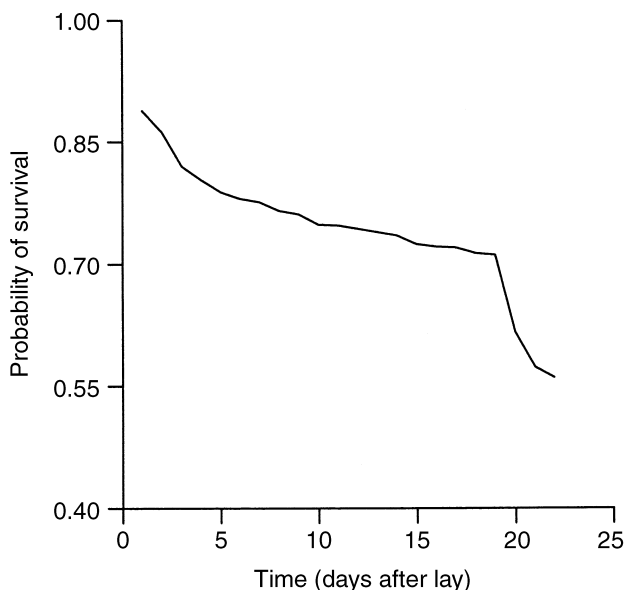


Fig. 1. Overall pattern of survival of houbara bustard eggs during incubation; 1992–1999. Mean incubation period is 23.5 days (SD = 0.9).

eggs; d.f. = 1, $P = 0.001$). However, when the potential effects of cohort, year of lay and breeding experience of mothers were entered as covariates, no significant difference was found between the two treatments ($X^2 = 0.450$, d.f. = 1, $P = 0.50$; $n = 436$ AI eggs; $n = 576$ PNI eggs).

Because we were not able to enter ‘mother’ into the model as a covariate, but mothers differed significantly in the hatchability of their eggs (\bar{x} eggs laid = 35.8, SD = 19.6, range = 14–86; covariates; year laid, incubation treatment; $X^2 = 118.42$, d.f. = 24, $P < 0.001$), we examined the proportions of females laying eggs with characteristically different probabilities of hatching, that were assigned to the two treatments. Eggs laid by each of the 25 females were given a rating depending on the K-M probability at the end of incubation, controlling for incubation treatment and year of lay: <0.30 was rated as a 1, 0.31–0.40 as 2, 0.41–0.50 as 3, 0.51–0.60 as 4, 0.61–0.70 as 5, and >0.71 as 6. Proportionately more (76% cf. 24%) eggs characterized by poor potential survival (rating categories 1 and 2) had been assigned to the treatment involving no incubation by females, while proportionately more (56% cf. 44%) eggs characterized by good potential survival (rating categories 5 and 6) had been assigned to the treatment involving some incubation by females ($X^2 = 35.6$, d.f. = 5, $P < 0.001$).

Effect of year of lay and cohort

Survival of eggs also varied depending on the year of lay (covariate: cohort, $X^2 = 64.9$, d.f. = 7, $P < 0.001$; Fig. 2), and the cohort (covariates: experience, year, age of mother; $X^2 = 72.02$, d.f. = 10, $P < 0.001$). The cohorts laying eggs with highest survival were the 1995 ($n = 96$), 1996 ($n = 51$) and 1997 ($n = 92$) cohorts; survival was lowest among eggs laid by the 1986 ($n = 88$), 1987 ($n = 196$) and 1988 ($n = 217$) cohorts, and intermediate for the 1991 ($n = 99$), 1992 ($n = 164$), 1993 ($n = 183$) and 1994 ($n = 69$) cohorts.

Survival after hatching

Survival between hatching and 3 years of age ($n = 1135$ hatchlings) showed an initial peak in mortality occurring within 6 months after hatching (75% survival of hatchlings), followed by a steady attrition: by the time birds were 3 years old survival was 69.2%, and by 10 years it was 42.8 (Fig. 3). Males were more likely to die than females between hatching and 3 years of age (covariates: year of hatch, cohort; $X^2 = 5.38$, d.f. = 1, $P = 0.02$, $n = 344$ males, $n = 360$ females; Fig. 4).

Causes of death

Causes of death were divided into those that occurred almost entirely within 6 months of hatching (neonatal, human-related, impactions and perforations, congenital), and those that occurred throughout the birds’ lives (Fig. 5). Causes of death differed significantly in their timing and magnitude ($X^2 = 288.6$, d.f. = 7, $P < 0.001$).

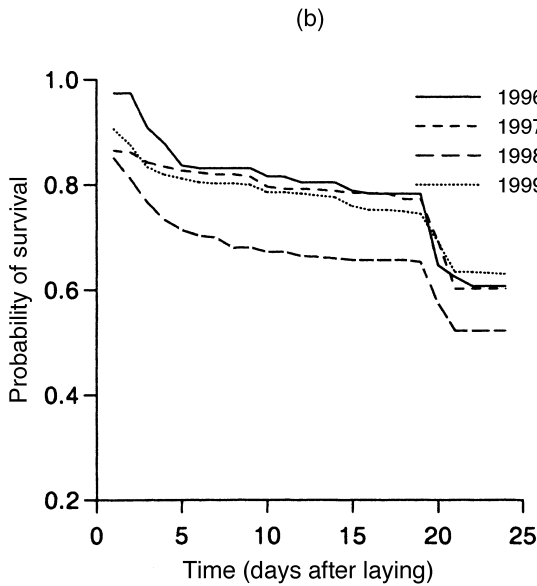
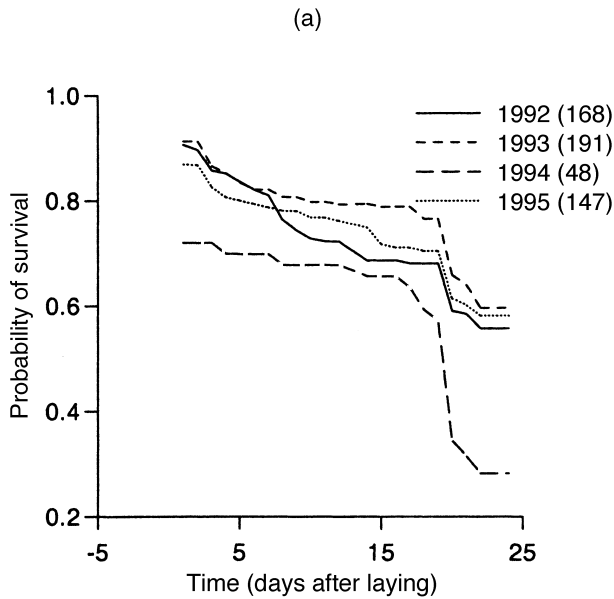


Fig. 2. Comparison of survival of houbara bustard eggs laid in the years 1992–1995 (a) and 1996–1999 (b). Sample sizes are given in brackets. Mean incubation period is 23.5 days (SD = 0.9).

Of 457 recorded causes, 16% were due to trauma ($n = 73$), 13% to infectious diseases ($n = 61$), 12% to some other cause ($n = 54$), 8% were neonatal ($n = 38$), 7% were human-related ($n = 31$), 5% were due to impactions and perforations ($n = 25$), 4% were attributed to congenital problems ($n = 19$), 4% to metabolic problems ($n = 19$), and 30% ($n = 137$) to unknown causes (no necropsy or no evident cause of death). There was no difference in the proportions of males and females dying from any of these causes ($X^2 = 5.98$, d.f. = 7, n.s.).

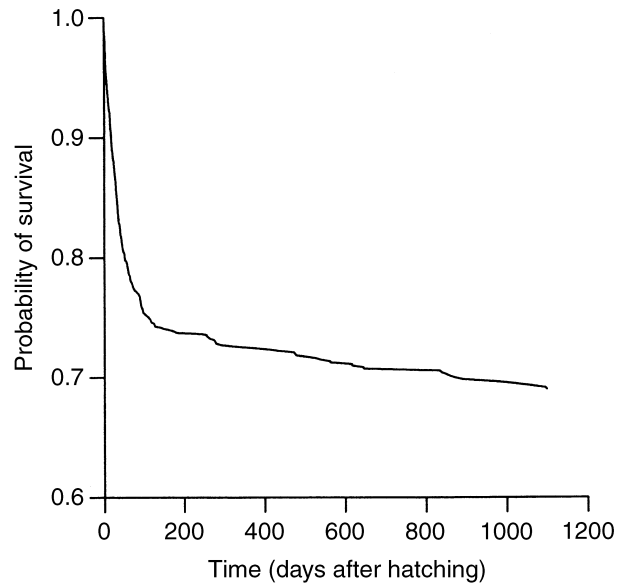


Fig. 3. Survival of captive houbara bustards from hatching until 3 years of age.

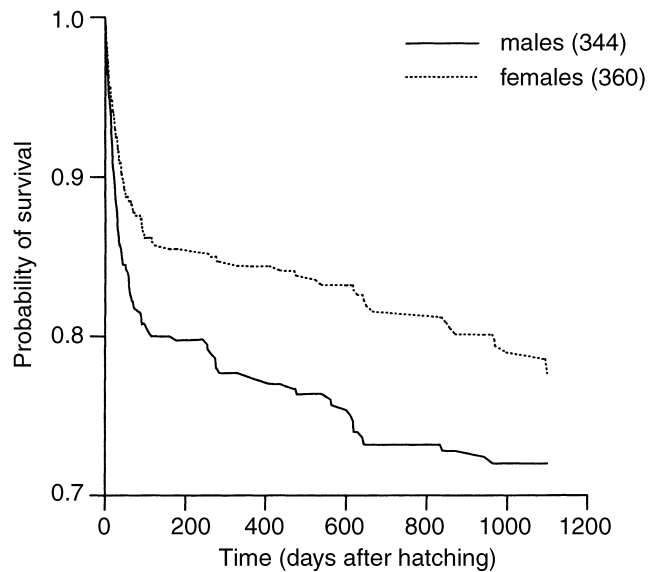


Fig. 4. Survival of male and female houbara bustards between hatching and 3 years of age. Sample sizes are given in brackets.

Effect of parents, year of hatch and cohort

Variations in survival of offspring of 19 mothers during the first 6 months after hatching were close to significance (covariates: year of hatch, incubation treatment; $X^2 = 28.7$, d.f. = 18, $P = 0.053$), but there was no difference at 3 years of age. No difference was found between survival of hatchlings from different fathers.

There were significant differences between years (1992–99) in survival up until 6 months of age ($X^2 = 25.68$, d.f. = 7, $P < 0.001$; Fig. 6), but no differences in survival of chicks hatched by different cohorts over the same period ($X^2 = 10.54$, d.f. = 9, n.s.).

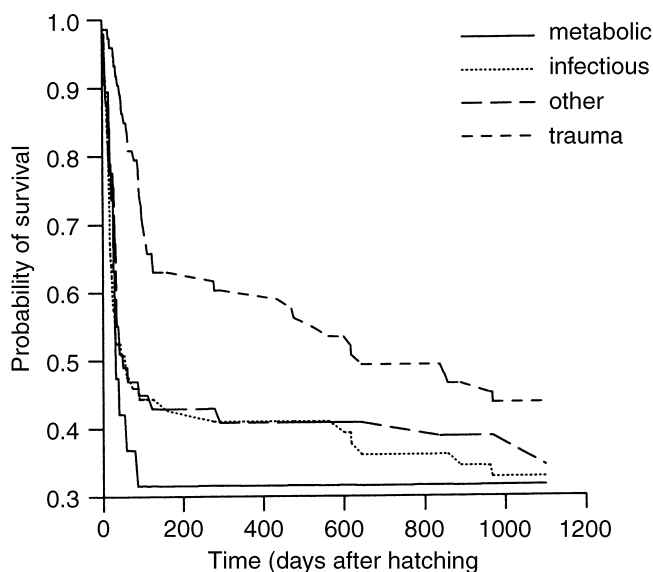


Fig. 5. Most common causes of death in the houbara bustard flock: hatching to 3 years of age.

DISCUSSION

Principal periods of mortality

Survival analyses identified two mortality peaks, the first during incubation and the second within 6 months after hatching. In recent years survival during incubation has tended to be higher (67% in 1999 and 59% in 1997 of assumed fertile eggs) but not consistently so (51% in 1998). About 73% of hatched chicks survived the first

year in captivity, and about 32% of inseminated eggs could be expected to result in 3-year-old birds, the median age of recruitment into the breeding population.

Two significant sources of variation in survival of eggs and chicks identified in these analyses were largely attributable to management practices, and therefore potentially reducible: variation between years (since the only parameters that vary between years, other than climate, are controlled by managers), and between eggs laid by different cohorts. Individual variation between mothers is probably beyond the control of management.

Survival during incubation

Main periods of egg loss occurred during the first 5 days and just prior to hatching. Uncertainty as to whether early losses are embryo deaths or undetected infertile eggs creates the management problem of where efforts should be directed to reduce these losses. Precise fertility and hatchability rates are unknown, ranging between 77% and 93%, and 53% and 69% respectively, depending on how early losses are interpreted. If early losses are embryo deaths, then mean hatchability is low compared with other wild species: 96% in mountain quail (*Oreortyx picta*), 93% and 86% in northern bobwhite (*Colinus virginianus*), 96% in grey partridge (*Perdix perdix*) (summarized in Johnsgard, 1988), 82.5% in red grouse (*Lagopus lagopus*), 90.5% in ptarmigan (*Lagopus mutus*), 91% in red-legged partridge (*Alectoris rufa*) and 85% in capercaillie (*Tetrao urogallus*) (summarized in Cramp *et al.*, 1980). If early identification of the reason for egg loss is technically difficult, then a double-headed

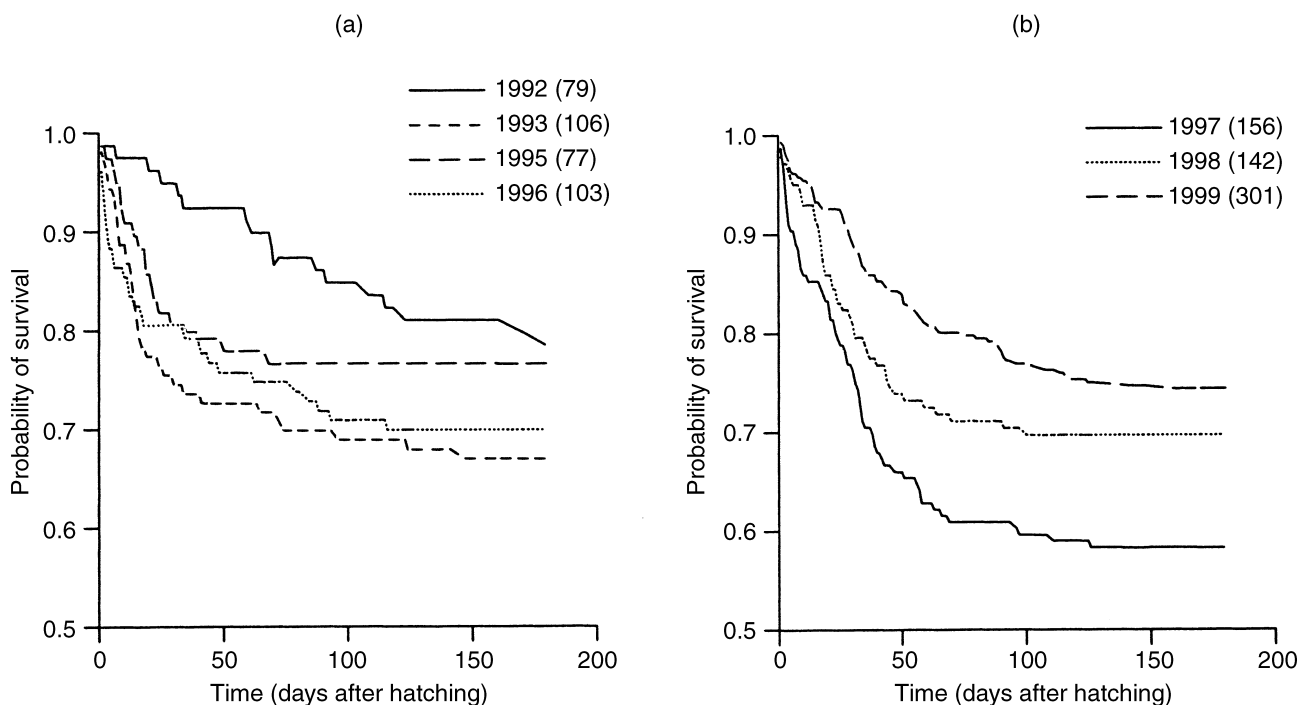


Fig. 6. Survival of captive houbara bustards during 6 months after hatching for chicks hatching in years 1992–1996 (a) and 1997–1999 (b). Sample sizes are given in brackets.

approach, systematically examining insemination and incubation protocols, might yield best results.

Pre-hatching losses are usually a result of deficiencies in the incubation environment: in artificially incubated trumpeter swan eggs (*Cygnus buccinator*) late mortality was attributed to fluctuations in the incubator environment (Hamilton *et al.*, 1999). Because hatchability of eggs depends on many factors (summarized in Hamilton *et al.*, 1999), systematic monitoring of all aspects of the incubation environment, as well as necropsies of dead embryos is essential before conclusions can be drawn.

Differences in survival between years and between eggs laid by different cohorts of females comprised a major source of variation that was most likely management related, and therefore potentially reducible. Unfavourable ambient temperatures during the 1994 season had a negative impact on the proportion of females breeding and their fecundity, and may have also affected hatchability (Saint Jalme *et al.*, 1996). Other than managing the entire flock in temperature-controlled facilities, there is probably little that can be done to address this problem.

Differences in survival of eggs laid by different cohorts imply that the rearing environment may influence subsequent productivity of breeding females. In captive zebra finches (*Taeniopygia guttata*) adult fecundity was correlated with juvenile body mass of females (Haywood & Perrins, 1992). Possible links between the rearing environment and future productivity in captive populations should be explored.

The importance of well-designed experiments to assess management efficacy, thereby avoiding expending unnecessary effort and resources, is illustrated by lack of support for partially incubating eggs under females. Initial trials and subsequent analyses of results failed to control for potential sources of variability in egg survival. Consequently the results do not discount the possibility that incubating eggs under females improves their hatchability, but neither do they support it.

Survival after hatching

Post-hatching survival dropped to 72.5% by the end of the first year, followed by a steady, slow attrition. It is difficult to judge what constitutes a 'reasonable' level of survival in captivity. First-year survival in 12 wild populations of relatively long-lived species (>10 y) averaged 49% (SD = 14.6%, range: 30–84%; Newton, 1989 and refs. therein; Piper, Boshoff & Scott, 1999; Schmutz & Ely, 1999; Wernham & Peach, 1999), but the primary factors responsible for mortality were most often predation and food availability, which do not apply to captive populations. While first-year survival of captive houbara bustards seems high, care should be taken when comparing wild and captive populations, as causes of mortality may be different, resulting in different selective pressures. If management-related, mortality in captive populations can result in selection for the captive environment, and therefore should be reduced. Causes of death and differences in survival between

sexes and years suggest that a proportion of this mortality is management related.

Despite strategies to minimize trauma-related deaths (wing-feather trimming, seclusion from visitors, soft-walled cages for juveniles), trauma was the primary cause of mortality, peaking before 4 months but continuing to kill birds irrespective of age. Traumatic injuries usually occurred when frightened birds tried to fly and collided with their cages. The early peak may represent a weeding-out of the most flighty individuals, implying selection for the captive environment, which may result in reintroduced birds with inadequate predator escape responses.

About 60% of deaths from infectious diseases occurred within 5 months of hatching. Young birds are susceptible to infectious agents as they undergo the transition from passive (maternal) to active immunity. They are also housed in larger groups, facilitating the spread of infectious diseases. Housing therefore influences likelihood of death, and the practice of housing males and females in different-sized groups and in different types of cages may have accounted for higher mortality among males. Deaths occurring in the first few weeks were often management related: neonatal deaths often result from incubation problems, and impactions and perforations result from the ingestion of sand and foreign objects. Congenital problems were few, reflecting the youth of the flock.

Although it is tempting to believe that current rates of mortality are 'incompressible', research may prove otherwise. For example, regular handling of a sample of chicks and juveniles reduced mortality in the first months after hatching by half (unpublished data). Regular evaluations of causes of death are critical to any attempt to improve survival, so necropsies should be routinely performed.

CONCLUSIONS

Critical to the assessment of survival and any attempt to reduce management-related mortality are: (1) exhaustive documentation, including life history data, management protocols and abiotic factors; (2) standardization of management practices; (3) regular project evaluation. These analyses allowed the identification of the timing of peaks of mortality, as well as sources of management-related variation that affect the survival and productivity of the captive flock. However, gaps in documentation prevented examination of important variables, such as paternity of dead embryos and infertile eggs, food quality, relatedness of founders and causes of death. Control groups, well-designed experimental trials and regular analyses should be used to assess patterns of mortality, and the efficacy of management practices designed to improve survival.

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