Realistic levels of inbreeding depression strongly affect extinction risk in wild populations

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ABSTRACT

The role of inbreeding depression in the extinction of wild populations is controversial, largely because there are no quantitative estimates of its impact using realistic levels of inbreeding depression. To address this deficiency, this study (1) provides a comprehensive estimate of the impact of inbreeding depression on wild, mammalian and avian species via a meta-analysis, and (2) determines the impact of this level of inbreeding depression on extinction risk over a broad taxonomic range via stochastic computer projections with and without inbreeding depression for populations with carrying capacities of 100, 500 and 2000 individuals. An average overall effect of 12 diploid lethal equivalents was found across the life-history of the species in the meta-analysis. In the stochastic computer projections, 12 diploid lethal equivalents of inbreeding depression (with purging) decreased median times to extinction by an average of 37%. These decreases were significant and of very similar magnitude, regardless of the carrying capacity modelled. Disregarding the influence of inbreeding depression on extinction risk will lead to serious overestimates of the survival prospects of threatened mammalian and avian taxa. Further, inappropriate recovery plans may be instituted if the causes of extinction risk and their relative contributions are not recognized.

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1. Introduction

Wild species can be driven to extinction by both deterministic factors (habitat loss, overexploitation, pollution and introduced species) and stochastic factors associated with small population size (demographic, genetic and environmental stochasticity, and catastrophes) (World Conservation Monitoring Centre, 1992; Baillie et al., 2004). However, most extinctions seem to result from the combined effects of both deterministic and stochastic processes (Lande et al., 2003; Reed et al., 2003b; O'Grady et al., 2004b).

Genetic stochasticity encompasses inbreeding depression, loss of potentially adaptive genetic diversity, and mutation accumulation (Frankham et al., 2002; Reed, 2005). Inbreeding depression is the most immediate and potentially damaging of these (Frankham et al., 2002; Vilas et al., 2006). Essentially

all well studied naturally outbreeding species show depressed reproductive fitness in inbred individuals, termed inbreeding depression (Falconer and Mackay, 1996; Lacy, 1997; Lynch and Walsh, 1998; Hedrick and Kalinowski, 2000). This has been demonstrated for wild (Crnokrak and Roff, 1999), laboratory (Bijlsma et al., 2000; Frankham et al., 2002; Reed et al., 2002, 2003a), and zoo (Ralls et al., 1988) populations. While there has been scepticism about the occurrence of inbreeding depression in wild populations, compelling evidence now exists. Of 157 valid data sets across 34 taxa reviewed by Crnokrak and Roff (1999), 90% showed deleterious effects due to inbreeding (Frankham et al., 2002).

The contribution of inbreeding depression to the extinction risk of wild species has been the subject of a long-running controversy. It has been argued that inbreeding plays little role in extinction as demographic and environmental stochasticity will drive small populations to extinction before genetic factors become important (Lande, 1988; Caro and Laurenson, 1994; Caughley, 1994; Dobson, 1999). An explicit meta-analytical test of this hypothesis based on 170 pair-wise comparisons of genetic diversity in threatened and taxonomic related non-threatened species showed that the majority of threatened species are not driven to extinction before genetic threats affect them adversely (Spielman et al., 2004).

Inbreeding depression has been linked with population declines and/or extinction of wild (Vrijenhoek, 1994; Newman and Pilson, 1997; Saccheri et al., 1998; Westemeier et al., 1998; Madsen et al., 1999, 2004) and captive (Frankham, 1995; Bijlsma et al., 2000) populations. These studies discussed individual cases, but none provided comprehensive evidence covering a wide range of threatened species, or gave a clear perspective on the circumstances under which inbreeding is important, and when it is not.

Studies of the impacts of inbreeding on extinction risk in wild populations are hampered by the difficulties in separating genetic and non-genetic components. Further, constraints on time and resources have forced past studies to concentrate on only a few, high profile species. Stochastic computer simulations are standard heuristic tools in population biology (Levins, 1966) and are widely used for predicting the fate of threatened populations by projecting life-history and environmental information forward in time (Akçakaya and Sjögren-Gulve, 2000; Beissinger and McCullough, 2000; Menges, 2000). Thus, stochastic computer projections offer the only feasible means for comprehensively and promptly investigating the role of inbreeding on extinction risk across a broad range of taxa (Brook et al., 2002). They allow many species to be investigated, can be performed relatively quickly, and allow the inclusion or exclusion of inbreeding in concert with demographic and environmental stochasticity; this is impossible in field experiments.

Computer projections have been used to investigate the effects of inbreeding depression on population growth and/or extinction risk. Some have found that inbreeding depression had strong effects (Vucetich and Waite, 1999; Oostermeijer, 2000), while some reported little impact on population viability (Burgman and Lamont, 1992). Others found that the impact depended on population size (Dobson et al., 1992), and that the impact was strongly affected by the

interaction between inbreeding, population size, and carrying capacity (Thévenon and Couvet, 2002). However, these studies focused on specific or hypothetical cases and were often projected for a few generations only. Whether these specific results hold for a broader taxonomic range requires evaluation.

The sole published study across a broad taxonomic range (birds, mammals, plants and reptiles) found a clear reduction in population viability (Brook et al., 2002) by applying a very conservative level of inbreeding depression; the average level found for juvenile survival in captive mammals (Ralls et al., 1988). Yet inbreeding depression affects all components of the life cycle (Frankel and Soulé, 1981; Keller, 1998; Frankham et al., 2002). Further, inbreeding depression is typically greater in more stressful wild environments than in more benign captive ones (Armbruster and Reed, 2005). For example, Crnokrak and Roff (1999) reported that inbreeding depression was seven times higher in the wild than in captivity. For these reasons, the reduction in population viability reported by Brook et al. (2002) is likely to be a serious underestimate.

The objectives of this work were to (1) undertake a meta-analysis of the literature to determine the full impact of inbreeding depression on the fitness of wild species; and (2) evaluate the effect of this level of inbreeding depression on extinction risk for 30 species using stochastic computer models.

2. Methods

2.1. Meta-analysis for the effects of inbreeding depression

An extensive literature search was undertaken for studies measuring inbreeding depression for natural populations in wild habitats. To match the aims of this study, only data from wild species were analysed (Table 1). The published data allowed resolution of the number of lethal equivalents (LEs) per haploid genome (β) for three vital rates viz. fecundity, first year survival (0–1 year old), and survival to sexual maturity (1 year old to age of sexual maturity). Where possible, β-values were estimated (Morton et al., 1956) for each of these rates from the regression of survival (S) on the inbreeding coefficient (F), as follows:

$$-\ln S = A - \beta F$$

where A is a constant.

Where there were only two categories of data, inbred and non-inbred, the following relationship (Crnokrak and Roff, 1999) was used to estimate β:

$$\beta = (-\ln[X_I/X_o])/F$$

where X_I is the rate for inbred individuals, X_o is the rate for non-inbred individuals, and F is the inbreeding coefficient for the individuals at which the rate was measured. A mean β-value was calculated for each of these rates by weighting each data set by the square root of its sample size. These calculated β-values are reported as diploid lethal equivalents (2β) in Table 1 for comparison to the familiar standard of 3.14 diploid lethal equivalents found by Ralls et al. (1988) for juvenile survival in zoo populations.

Table 1 – The number of diploid lethal equivalents (2β) estimated to affect fecundity, first year survival (0–1 year old), and survival to sexual maturity (1 year old to age of first reproduction)

Species	2β	N	Reference
A: Fecundity			
Cervus elaphus	2.69	209	Slate et al. (2000)
Gambusia holbrooki	8.072	14	Leberg (1990)
Melospiza melodia	2.516	161	Keller (1998)
Mus domesticus	5.65	144	Meagher et al. (2000)
Weighted mean	3.936		
B: First year survival			
Gallinula chloropus	4.342	72	McRae (1996)
Geospiza fortis	4.29	2040	Gibbs and Grant (1989)
Lenontopithecus rosalia	4.65	481	Dietz et al. (2000)
Melospiza melodia	2.88	1091	Keller (1998)
Parus major	1.23	7346	Greenwood et al. (1978)
Parus major	1.474	1297	van Noordwijk and Scharloo (1981)
Piciodes borealis	0.74	745	Daniels and Walters (2000)
Weighted mean	2.354		
C: Survival to sexual maturity			
Aphelocoma ultramarina	>13.44	858	Brown and Brown (1998)
Geospiza fortis	8.816	918	Gibbs and Grant (1989)
Melospiza melodia	2.64	1127	Keller (1998)
Parus major	3.73	616	Greenwood et al. (1978)
Piciodes borealis	1.08	795	Daniels and Walters (2000)
Weighted mean	5.968		

When determining these mean β-values (see Section 2), the contribution of each data set was weighted by the square root of its sample size (N).

2.2. The species modelled

The stochastic modelling encompassed 18 mammal and 12 bird species of varied ecologies (carnivores, herbivores, omnivores), geographical regions (Africa, America, Asia, Europe, and Oceania), generation lengths (range 2–22 years) and population growth rates (deterministic $r = -0.214$ to $+0.253$), for which robust population models had already been constructed in previous works (Brook et al., 2000; Reed et al., 2003b; O'Grady, 2002; O'Grady et al., 2004a,b). Fifty seven percent (17) of the species modelled are Red Listed by the World Conservation Union (Baillie et al., 2004) as threatened. The species are listed in Table 2. The data sources for the species modelled in this study are published in Brook et al. (2000), Reed et al. (2003b), O'Grady (2002), O'Grady et al. (2004a,b). Similarly, the population models used in this study were drawn from these aforementioned studies, but modified as described in Section 2.3 to account for the full effects of inbreeding depression.

2.3. Stochastic computer modelling

The program VORTEX v8.41 (Miller and Lacy, 1999) was used to model the impacts of inbreeding depression on extinction risk. The models were parameterised using the protocols prescribed for this program (Miller and Lacy, 1999), and as described in a previous study which evaluated the predictive capacity of this program (Brook et al., 2000). These models incorporated all published factors known, or suspected by field experts to influence each species' extinction risk. All models incorporated the effects of genetic, environmental, demographic and catastrophic stochasticity, and were parameterised via long-term studies (>10 years data) published for the species. Each species was modelled at the time point where the most comprehensive data set was found to build its stochastic computer model. In some cases, these data sets no longer reflect the species' current circumstances. Thus, the extinction risks generated in this study are for heuristic purposes only and are not intended as prospective viability analyses applicable to conservation decision-making.

Based upon the meta-analysis, a total of 12 LEs per diploid genome were apportioned across the life span. All models incorporated the effects of natural selection (purging) reducing the frequency of deleterious alleles. To approximate observed proportions of inbreeding depression due to highly deleterious alleles and mildly deleterious alleles (Simmons and Crow, 1977), five lethal equivalents were assumed to be due to recessive lethal alleles and seven due to deleterious alleles of small effect. Hence, in the models five LEs were assumed to be due to recessive lethal alleles and therefore subject to purging. VORTEX allows purging of a maximum of 5 LEs through both selection and genetic drift (Miller and Lacy, 1999). The other seven lethal equivalents were modelled to be sub-lethal alleles of smaller effect that are little affected by purging. Four of these were modelled to reduce survival of juveniles until sexual maturity, and the remaining three to reduce fecundity. The term "lethal equivalents" is more commonly related to a reduction in survival in response to inbreeding rather than fecundity. In this study, "lethal equivalents" is related to fecundity as a short-hand for the slope in the log-linear model of inbreeding's effects on fecundity. In species where juveniles attained sexual maturity in one year, all β-values for survival were used to reduce survival of inbred individuals during that year. Where juveniles took more than one year to reach sexual maturity, the effect of the 4 LEs was divided equally across these years. For example, where a species took two years to reach sexual maturity, 2 LEs were applied to first year survival, and 2 to second year survival. The effect of these sub-lethal alleles was modelled by an exponential decline (Morton et al., 1956):

$$S = S_o e^{-\beta F}$$

where S is the value calculated by the model for the rate affected by inbreeding depression, S_o is the rate for non-inbred individuals, β is the average number of lethal equivalents per haploid genome, and F is the inbreeding coefficient automatically calculated (Miller and Lacy, 1999) for individuals by VORTEX.

Initial population sizes (N) of 50, 250 and 1000 were used, broadly corresponding to the IUCN Red List categories of Critically Endangered, Endangered and Vulnerable, respectively based on Criterion D of the Red List system (Baillie et al., 2004). Following the protocols of Brook et al. (2002), a ceiling carrying capacity (K) of twice the initial population size was imposed for most species. This is a less assumption-driven means of representing habitat limitation in the absence of

Table 2 – Impacts of inbreeding depression on median times to extinction for 30 species, based upon stochastic computer projections

Species	R_0	N = 50				N = 250				N = 1000			
		MTE_{noID}	$MTE_{3.14}$	MTE_{ID}	%Rdn	MTE_{noID}	$MTE_{3.14}$	MTE_{ID}	%Rdn	MTE_{noID}	$MTE_{3.14}$	MTE_{ID}	%Rdn
Aphelocoma coerulescens	0.324	16	11	9	44	53	31	21	60	127	63	42	67
Bubalus depressicornis	0.984	2	2	2	0	3	3	3	0	3	3	3	0
Bubo virginianis	1.976	3	3	3	0	5	5	5	0	7	6	6	14
Capra species	0.260	10	8	7	30	19	15	13	32	27	22	19	30
Cervus elaphus	0.723	2	2	2	0	4	4	4	0	6	5	5	17
Cervus eldii eldii	1.451	9	8	6	33	21	16	12	43	34	26	19	44
Charadrius melodus	1.084	8	7	6	25	17	14	12	29	26	23	19	27
Copsychus seychellarum	0.886	6	5	5	17	12	10	9	25	18	16	14	22
Delichon urbica	0.875	49	21	11	78	292	85	33	89	464	273	95	80
Dendroica kirtlandii	0.957	3	3	3	0	5	5	5	0	7	7	6	14
Dendrolagus matschiei	1.107	8	5	4	50	18	11	8	56	28	18	12	57
Gorilla gorilla beringei	1.452	7	6	5	29	13	11	9	31	19	16	14	26
Gymnobelideus leadbeateri	0.673	12	9	7	42	34	22	15	56	64	37	26	59
Leucopsar rothschildi	0.517	5	5	4	20	9	8	7	22	12	11	11	8
Lipotes vexillifer	0.020	2	2	2	0	4	4	4	0	5	5	5	0
Lycaon pictus	1.580	5	5	4	20	7	7	6	14	13	11	9	31
Lynx rufus	0.869	14	12	9	36	45	27	17	62	95	51	29	69
Marmota flavientris	0.885	5	5	4	20	11	9	8	27	14	13	11	21
Meles meles	0.997	7	6	5	29	14	11	10	29	19	17	14	26
Melospiza melodia	0.762	32	18	12	63	169	64	29	83	783	188	71	91
Mirounga leonia	0.921	11	8	6	45	44	21	13	70	84	38	24	71
Neophema chrysogaster	1.000	5	5	4	20	13	11	9	31	24	20	16	33
Oreamnos americanus	0.606	7	6	5	29	15	12	10	33	23	19	15	35
Panthera leo	0.972	11	7	6	45	38	19	12	68	88	36	21	76
Petaurus australis	1.352	14	10	7	50	52	27	18	65	144	63	36	75
Picoides borealis	1.039	10	8	6	40	25	18	13	48	42	30	22	48
Rhinoceros sondaicus	0.900	6	5	4	33	10	9	8	20	13	12	11	15
Streptopelia mayeri	1.662	6	6	5	17	11	10	9	18	15	13	13	13
Trichechus manatus latirostris	1.050	16	10	7	56	41	23	15	63	69	38	25	64
Zosterops lateralis chlorocephalia	0.823	22	12	9	59	98	35	20	80	319	52	42	87
Mean					31				39				41

R_0 is deterministic growth rate per generation. Median time to extinction (MTE) is measured in generations. Nine scenarios were modelled (i.e., three levels of inbreeding depression for each of three initial population sizes N = 50, N = 250, and N = 1000). The levels of inbreeding depression were: no inbreeding depression (noID), the full impact of 12 diploid lethal equivalents (ID), and the effect of 3.14 diploid lethal equivalents applied to juvenile survival only (3.14). The percent reduction in median time to extinction (%Rdn) due to inbreeding depression was also calculated for each of the 30 species.

detailed data required to estimate the additional parameters in density dependent models of vital rates (a common situation for threatened species). It also provides a conservative estimate of extinction risk as other functional forms of density dependence often strongly affect predicted risk (Ginzburg et al., 1990). However, where density dependence of the vital rates was detected for a particular species (Akçakaya, 1996; Miller and Lacy, 1999) it was modelled explicitly via a negative feedback on that vital rate instead of a ceiling carrying capacity.

Three levels of inbreeding depression were modelled for each initial population size. These were: no inbreeding depression, the full impact of 12 diploid lethal equivalents, and a partial effect of 3.14 diploid lethal equivalents applied to juvenile survival only to permit comparison with Brook et al. (2002) and other PVA simulations which commonly use this value as a default input. In this way nine scenarios were modelled. All stochastic simulations were replicated 1000 times. The simulations were projected forward to estimate median time to extinction for each species, median time to extinction being the time taken for half of the simulation replicates become extinct. Extinction was defined as no remaining animals of one sex. Median time to extinction was assessed as it has an unbounded scale, in contrast to the proportion extinct. In addition, this measure is not biased by occasional run times that are extremely long, which is a problem with mean time to extinction (Brook et al., 2002). Further, this variable was used as it is intuitively clear to most wildlife managers.

Median time to extinction was assayed in generations as extinction risk has been shown to scale better to generations than to years (Leigh, 1981; O'Grady, 2002; Frankham and Brook, 2004). Median time to extinction and probability of extinction were obtained and averaged across species for the nine scenarios modelled. Most analyses were performed using the percentage difference in median time to extinction (MTE) between the models for a species with inbreeding depression (MTE_{ID}), and without (MTE_{noID}), computed as ($[MTE_{noID} - MTE_{ID}]/MTE_{noID}$) * 100.

2.4. Statistical analysis

Non-parametric analyses were used for most analyses, as percent differences were not normally distributed. Wilcoxon signed rank tests were used to test whether differences for each of the three population sizes across all species, and across mammals and birds as groups, were significantly greater than zero. Variation in median time to extinction between mammals and birds was tested using a Kruskal–Wallis test, while differences among population sizes and among these broad taxonomic groups were compared using Friedman's test (Sokal and Rohlf, 1995). The relationship between the species' growth rates (measured as R_0) and the percentage difference in their median time to extinction was measured using Spearman's rank correlation and by linear regression. As the data were close to a normal distribution in this test, these two parametric tests were used not only as heuristic tools but to cross check the results of the other. As both gave identical conclusions, only the correlation analyses are reported. For all tests $\alpha = 0.05$. All tests were performed using MINITAB v12 statistical software (Ryan and Joiner, 1994).

3. Results

3.1. Meta-analysis of inbreeding depression

The meta-analysis revealed an overall inbreeding depression of 12.3 diploid lethal equivalents, consisting of 3.9 lethal equivalents for fecundity, 2.4 for first year survival (0–1 year old), and 6.0 for survival from 1 year old to sexual maturity (Table 1).

3.2. Stochastic computer projections to determine the impact of inbreeding depression on extinction risk

Inbreeding depression (12 LEs) markedly reduced the median time to extinction across the species (Table 2). All species showed a pattern of lower population size with inbreeding depression that translated into a higher probability of extinction. Representative population trajectories are shown in Fig. 1. Mean reduction in median time to extinction was 31%, 39% and 41% for initial population sizes of 50, 250 and 1000 respectively. These reductions in median times to extinction were all highly significant ($p < 0.001$) for each population size, though not significantly different between the three population sizes ($p = 0.459$). Similarly, these reductions were also highly significant for the three initial population sizes where mammals and birds were assayed separately as broad taxonomic groups (for all three mammalian N, $p < 0.001$; for birds, $p = 0.003$, $p = 0.003$ and $p < 0.001$ respectively).

There was a significant relationship between the species' growth rates and the reduction in their median time to extinction ($r_s = 0.580$, $p = 0.001$; $r_s = 0.594$, $p = 0.001$; and $r_s = 0.696$, $p < 0.001$ for initial N of 50, 250 and 1000, respectively). Species with the highest growth rates generally had the greatest reduction in their median time to extinction (Table 2).

No significant differences in median time to extinction were found between mammals and birds for the three initial population sizes ($p = 0.416$, $p = 0.314$, and $p = 0.309$, respectively) under the impact of 12 LEs. Similarly, the Friedman's test indicated that there were no significant differences in median time to extinction among population sizes and among these broad taxonomic groups ($p = 0.135$).

The effect of 3.14 LEs applied to juvenile survival only also reduced median time to extinction across all the species, though to a lesser degree than the realistic impact of 12 LEs. Average reductions in median times to extinction across all the species for the initial population sizes of 50, 250 and 1000 were 17%, 26%, and 28% respectively.

4. Discussion

This study provides the first realistic estimate of the impact of inbreeding depression on the fitness of wild mammals and birds across a broad taxonomic range. The estimated value of 12.3 diploid lethal equivalents is almost four times greater than that used in previous simulation studies. This modelled level of inbreeding depression markedly and significantly reduced the estimated median times to extinction compared to models lacking inbreeding depression. Unlike most simulation studies on the effects of inbreeding depression, this study encompasses the effects of purging. It extends the evidence on the role of inbreeding depression in extinction from
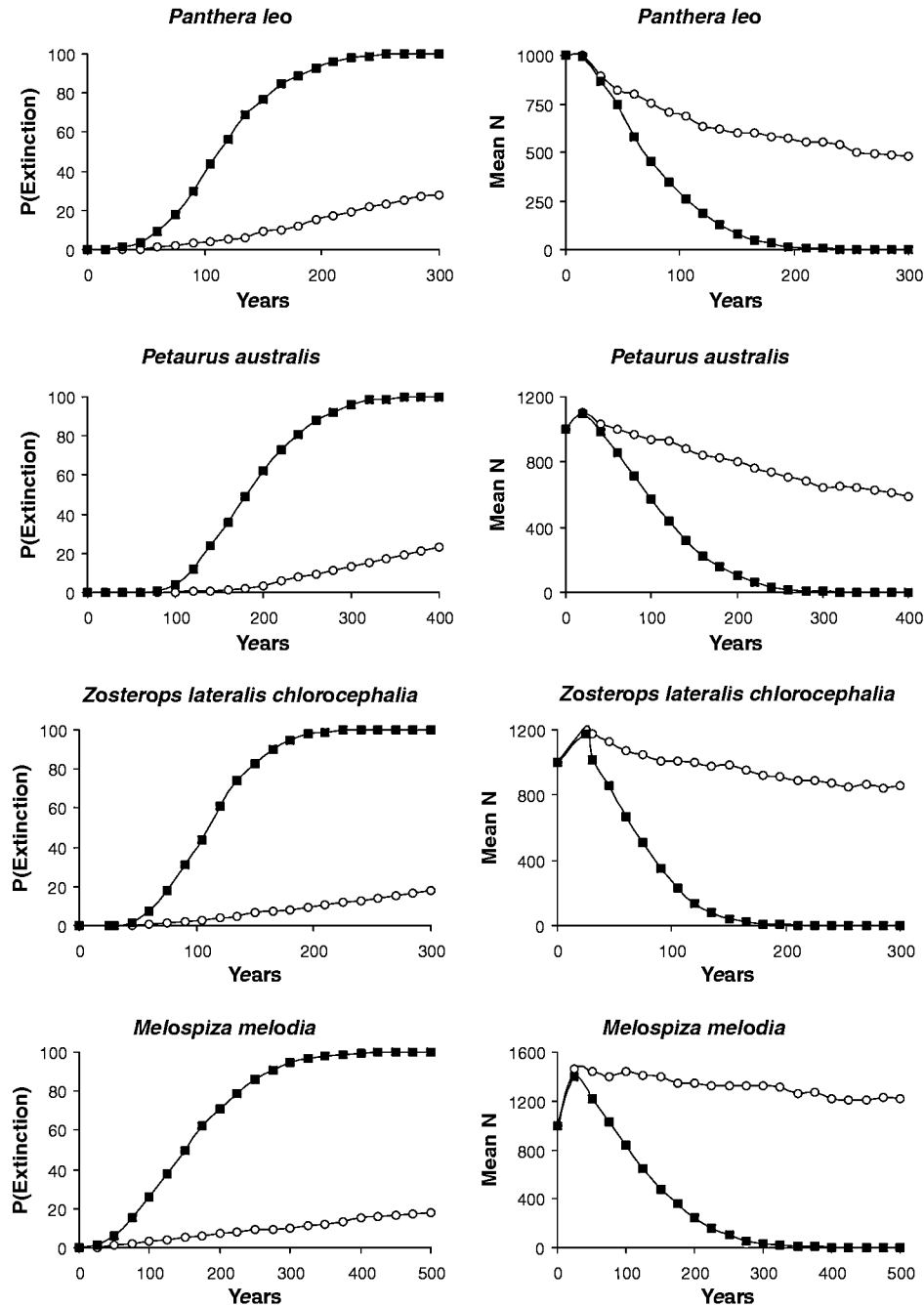
Fig. 1 – Impact of inbreeding depression (square data points) versus none (circles) on the cumulative probability of extinction (P[Extinction]) and mean final size (Mean N) for four representative species. These data were determined by stochastic computer models with all known demographic, environmental and catastrophic threats included and with an initial population size of 1000 (see Section 2).

hypothetical life-histories (Mills and Smouse, 1994) and a few real species (Dobson et al., 1992; Newman and Pilson, 1997; Saccheri et al., 1998; Oostermeijer, 2000) to a wide range of mammalian and avian taxa.

The mean level of inbreeding depression in juvenile survival found in this study is much less than that for the other two components of fitness viz. fecundity and survival to sexual maturity. Hence, the results of this study suggest that, in the absence of specific data, more severe default values for inbreeding depression (i.e. spanning the entire life cycle) should be applied in population viability analyses for species in the wild, or risk underestimating their probability of extinction. For example, the reductions in median time to extinction found in this study where 3.14 diploid lethal equivalents were applied to juvenile survival only were 17%, 26% and 28%, while 12 lethal equivalents produced reductions of 31%, 39% and 41% for the same suite of species and respective initial population sizes.

The findings in this study are corroborated by other lines of evidence for the role of inbreeding depression in extinction. Most endangered species have less genetic diversity than related non-endangered species (Spielman et al., 2004). If 'non-genetic' factors drove species to extinction before inbreeding was a problem, there would be no such difference. Further, loss of genetic diversity is related to reduced population fitness (Reed and Frankham, 2003).

Even with a comprehensive meta-analysis, these results are still likely to slightly underestimate the impact of inbreeding depression on extinction in wild populations. The total estimate of lethal equivalents for fecundity and survival in mammals and birds obtained from the meta-analysis agrees with the only comparable datum of the full number of lethal equivalents from an individual species (found by summing the individual components reported by Keller, 1998). However, the estimate found in this study may be conservative because it was not possible to resolve any effects of inbreeding depression on adult survival after first reproduction (see Section 2), and these effects may be important for long-lived, iteroparous species. In addition, the models assumed that all adults in each species are equally likely to reproduce. This does not apply in most wild populations (Frankham et al., 2002) leading to a smaller effective population size and potentially greater inbreeding. Consequently, the results of this study are likely to underestimate the impact of inbreeding depression.

In what circumstances is inbreeding depression likely to make important contributions to extinction risk? The level of inbreeding depression applied in this study produced a near ubiquitous decrease in median time to extinction across all the population sizes modelled, for both mammals and birds, and for a wide range of life-histories. Thus, the results in this study indicate that inbreeding depression is a major threat for most mammalian and avian taxa at small to moderate population sizes (i.e., less than a few thousand individuals). However, the meta-analysis showed some variation among species in the severity of inbreeding depression (Table 1). Species with lower genetic loads would likely be relatively more resistant to this threat.

Inbreeding depression may have little time to affect populations declining rapidly due to deterministic pressures, such as habitat loss (Brook et al., 2002). For example, at the time two of the species within this study (viz. *Bubalus depressicornis* and *Lipotes vexillifer*) were assessed by the World Conservation Union, both were experiencing substantial anthropogenic threats (Manansang et al., 1996 and Kaiya et al., 1994 respectively). Both had highly negative growth rates such that inbreeding depression did not foreshorten their estimated median time to extinction at any population size modelled (Table 2). This study, like that of Brook et al. (2002), found a significant positive relationship between population growth rate (r) and reduction in median time to extinction (Table 3). However, compared to the study of Brook et al. (2002), this study found a smaller reduction in median time to extinction due to inbreeding depression as the species' population growth rate (r) decreased (Table 3). The smaller reduction in median time to extinction found in this study is largely a consequence of the greater deterministic pressures faced by some species in this study compared to those faced by the species in Brook et al. (2002). These deterministic pressures

Table 3 – Panel A: the relationship between population growth rate per generation (R_0) and reduction in median time to extinction measured in generations (MTE) due to a modelled inbreeding depression of 12 diploid lethal equivalents [three initial population sizes (N = 50, N = 250, and N = 1000) were modelled]; Panel B: a comparison of the relationship between initial population growth rate (r) and reduction in median time to extinction measured in years (MTEy) at an initial population size of 250 individuals found in this study $Ba250$ and by Brook et al. (2002) $Bb250$

N	Regression	r^2 (%)	p
Panel A			
50	Percent reduction MTE = 7.8 + 24.2R_0	22	0.006
250	Percent reduction MTE = 9.1 + 30.7R_0	19	0.009
1000	Percent reduction MTE = 7.0 + 35.1R_0	26	0.003
Panel B			
Ba250	Percent reduction in MTEy = 0.64 + 2.14r	42	<0.001
Bb250	Percent reduction in MTEy = 0.46 + 4.42r	72	<0.001

sharply reduced the growth rate of some species in this study (Table 2) and overwhelmed or dominated the influence of inbreeding depression on their median time to extinction.

Inbreeding will have less impact on naturally inbreeding species, as they express lower inbreeding depression on average due to long-term purging of the genetic load (Husband and Schemske, 1996). Populations that have had a very small effective population size for a long period of time, or those that have recovered from population bottlenecks, should be less sensitive to inbreeding depression due to purging of deleterious recessive alleles, though the effects of purging are usually relatively small (Lacy and Ballou, 1998; Byers and Waller, 1999; Miller and Hedrick, 2001; Frankham et al., 2001; Crnokrak and Barrett, 2002; Reed et al., 2003a). Inbreeding impacts will probably be less in species with polyploid ancestry, as they seem to suffer less inbreeding depression than equivalent diploids due to a lower frequency of homozygotes (Husband and Schemske, 1997; Frankham et al., 2002).

Inappropriate recovery programs may be devised if realistic levels of inbreeding depression are not taken into account. There are at least three major reasons for this. First, reproductive fitness is often improved if inbred populations are outcrossed (Vrijenhoek, 1994; Westemeier et al., 1998; Madsen et al., 1999; Ebert et al., 2002; Vilà et al., 2003; Schwartz and Mills, 2005). If this is not done, an inbred population with low fitness may continue to decline, as happened with the Illinois population of the greater prairie chicken (*Tympanuchus cupido pinnatus*; Westemeier et al., 1998). Attempts to recover the population by habitat improvement failed to halt its decline, and it only recovered following outcrossing with another population.

Second, as shown in this study, even moderately large populations (initial N = 1000) are susceptible to the deleterious effects of inbreeding, and are unlikely to be viable over the long-term. This result accords with stochastic computer modelling by Reed et al. (2003b) who concluded that populations of similar size to those studied here are unlikely to be viable in the long-term (40 generations). Further, this study shows that the relative impact of inbreeding on median time to extinction is similar over a range of different population sizes

of general relevance to conservation biology (i.e., a few thousand or less, although the absolute value of median time to extinction increases as population size increases). For such moderately small populations, the results of this study indicate that there is often a time lag until inbreeding accumulates and increases extinction risk (Fig. 1). Thus, the management of genetic threats attending small population size should not be postponed in the expectation that if the species has persisted at a certain size for a few decades then inbreeding depression will not substantially affect its viability, or hasten its median time to extinction.

Third, funding priorities for conservation and restoration will be distorted if the impacts of different factors on extinction risk are not correctly understood. The greater prairie chicken mentioned above is a good example. As recounted by Westemeier et al. (1998), management strategies were initially focussed on non-genetic recovery methods to recover a decline in population size and reproductive fitness. However, despite these efforts the population continued to decline until genetically unrelated individuals were introduced. These introductions subsequently restored egg viability.

In conclusion, realistic levels of inbreeding depression markedly elevate extinction risk for most threatened mammalian and avian taxa. These results emphasise the importance of avoiding inbreeding and maintaining genetic diversity in threatened species.

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