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The effects of group versus intensive housing on the retention of genetic diversity in insurance populations

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Abstract

Background: Retention of genetic diversity and demographic sustainability are the cornerstones of conservation breeding success. In theory, monogamous breeding with equal reproductive output will retain genetic diversity in insurance populations more effectively than group housing which allows mate choice or intrasexual competition. However, the ecological relevance of group housing to a species can outweigh the theoretical benefits of forced monogamy. Here we investigated the influence of different types of captive housing (group (mate choice) versus intensive (forced monogamy)) on reproductive success, litter size and genetic diversity in the endangered Tasmanian devil (*Sarcophilus harrisii*).

Results: For male Tasmanian devils, the proportion of individuals that failed to reproduce was significantly greater in group (maximum 10 individuals) than intensive housing. This suggests greater genetic diversity is retained when devils are bred in intensive housing. For male devils, body weight predicted reproductive success in group housing, suggesting certain individuals are dominant due to a larger body size, leading to unequal genetic contribution. We then used simulation models to predict rates of decline in genetic diversity and inbreeding accumulation over time comparing group and intensive housing. When managed independently, empirically observed reproductive outputs were predicted to result in large accumulations in inbreeding and loss of gene diversity in both housing types, although these effects were greater in group housing. Transferring individuals between the housing facilities decreased inbreeding accumulation and increased gene diversity in both housing types highlighting the importance of managing independent zoo populations collectively.

Conclusions: If conservation programs wish to provide mate choice opportunities through group housing, the impact intrasexual competition will have on dominance and sequential reproductive opportunities needs to be understood prior to commencement. Group housing is becoming increasingly topical as it provides potential ecological benefits, may decrease mate incompatibilities and increase offspring fitness, however it can also result in the loss of genetic diversity in already genetically depauperate species.

Keywords: Mate choice, Conservation, Tasmanian devil, Insurance population

Background

Many threatened species require some form of population management as a conservation tool to prevent extinction. Topical reviews have found that conservation breeding or insurance populations have recently played a role in threat level reduction of endangered species [1, 2]. Combined with in-situ management, insurance populations prevent extinction until wild reintroductions are achievable as seen with California condors, *Gymnogyps californianus* [3], golden-lion tamarins, *Leontopithecus rosalia* [4] and black-footed ferrets, *Mustela nigripes* [5]. The primary goal of an insurance population is to capture and maintain representative wild genetic diversity, as well as maintain demographic stability, for as long as possible [6–8]. Population genetic diversity has individual fitness benefits (e.g. reproductive success), in addition to population fitness benefits (e.g. potential to adapt to environmental changes), both being important for populations to be used as sources for release to the wild [9]. Typically, insurance

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populations commence when a species is in dire straits and so accessing suitable numbers of unrelated founders is problematic as populations are usually fragmented and declining. Genetic diversity in captivity is further lost when founder representation is unequal [10]. For decades the global zoo community has utilized a mean kinship strategy (the average relatedness of an individual to the population, calculated via pedigrees), pairing individuals who are least related to each other to maintain genetic diversity [11, 12]. Traditionally this meant that individual pairs were housed together for breeding purposes, a type of forced monogamy, regardless of the species life history and without the option of mate choice. This practice of forced monogamy is not realistic for all species (e.g. giant panda [13]), and often deviates from the natural ecology of the species' wild habitat, so recent discussion has occurred around whether providing mate choice, via group housing of multiple individuals, to improve conservation breeding [14].

The literature provides numerous illustrations of difficulties in conservation breeding and the resulting impact on genetic diversity. Higher reproductive outputs from certain individuals results in higher genetic contributions to subsequent generations, and lower genetic contributions from less successful individuals [15]. For example, in the clouded leopard (*Neofelis nebulosa*), incompatibilities among forced breeding pairs (aggressive behaviour resulting in death or serious injury) created unequal founder representation, as only 27% of males and 20% of females successfully reproduced [16]. Furthermore, genetic diversity can also be lost as a result of genetic drift in small, finite populations [9]. Genetic drift becomes increasingly influential with decreasing population sizes and insurance populations tend to be small in size [17]. In the absence of selection from inadequate resources, disease and harsh weather, often encountered in a species' natural habitat, genetic drift leads to random fixation and loss of alleles in insurance populations [18]. Simulations with population sizes similar to those considered ideal for insurance populations demonstrated that genetic drift can rapidly deplete genetic diversity; however, the immigration of only a few individuals annually had the potential to slow or halt the effects of genetic drift [18]. The loss of genetic diversity arising from these two processes, mate incompatibilities and genetic drift, impedes conservation goals.

In conservation breeding, allowing mate choice may avoid reproductive failure that results from incompatible mate pairing, as breeders will have opportunity to select preferred mates, increasing overall productivity of the population. Mate choice can increase offspring fitness (quantity or quality) via direct behavioral benefits (parental investment) or indirect genetic benefits (parental compatibility) [19, 20]. In some species the reproductive rate of genetically desired individuals that fail to breed when force-paired, have increased with the addition of mate-choice management (e.g. cheetahs, *Acinonyx jubatus* [21] and zebra finch, *Taeniopygia guttata* [20]). A potential downside of allowing mate choice in an insurance population is increased reproductive skew among individuals. If certain individuals are consistently chosen as the preferred mate, it can result in the exclusion of non-preferred individuals [14] leading to unequal founder representation and loss of genetic diversity [22]. Unequal founder representation in insurance populations occurs when certain founding individuals have low to absent genetic contributions to the subsequent generations in captivity, resulting in their genetic line being poorly represented relative to others, or completely extinguished. When founding lines become extinguished, the population has reduced adaptive potential, and so maintaining equal founder representation increases the likelihood of adaptation to novel environments, diseases and pollutants. Long-term survival for small populations can be potentially compromised if management is exclusively based on mate-choice breeding.

A manner in which to approach these issues in conservation breeding programs is to create a captive environment similar to a species' wild environment which enables the inclusion of both mate-choice breeding preferences and some pedigree-based breeding. That is, housing low mean kinship, unrelated individuals together in group enclosures allows for individual mating preference to take place while still moderately controlling for equal genetic representation. Experimentally determining mate-choice preferences prior to breeding is logistically unachievable for large-scale insurance populations. As such, housing selected individuals in groups may be a way forward for conservation breeding that is efficient and financially achievable, minimises behavioural adaptation whilst boosting breeding success. In addition, reproductive success may improve as a result of mate preferences and intrasexual competition. A characteristic of male (and to a lesser degree, female) reproductive success is mate acquisition ability [23, 24]. Individuals in group enclosures therefore may obtain a disproportionately high reproductive output as a result of social hierarchies in addition to mate-preferences [14]. Until recently, it has been difficult to explore these evolutionary processes in respect to conservation management, given the unknown complexity of mate choice across taxa and the logistic requirements within a captive-breeding setting.

In this study, we compare two conservation breeding approaches 1) forced monogamous pairings to equalize founder representation, and 2) opportunity for mate-choice. We use the Tasmanian devil (*Sarcophilus harrisii*) insurance metapopulation to assess how alternate management strategies, group housing (mate choice) versus

intensive housing (forced monogamy), impact reproductive success and genetic representation. The Tasmanian devil has recently suffered a severe population decline (~85%) after the emergence of two transmissible cancer variants, Devil Facial Tumour 1 (DFT1) and Devil Facial Tumour 2 (DFT2), first observed in 1996 and 2015 respectively [25, 26]. An insurance population was established in 2006 under the management of the Save the Tasmanian Devil Program (STDP) in collaboration with the Zoo and Aquarium Association (ZAA), to provide insurance against extinction, while in situ conservation focused on disease control [27]. Initial breeding in the insurance population was through intensive housing, with free-range enclosures (22 ha) commencing in 2009, group housing (2–3 ha) commencing in 2011 and an island population (120 ha) in 2012 [27].

We had three overall aims for this study. Firstly, we used pedigree data to determine the influence of intensive housing and group housing on reproductive success and litter size in the insurance population. Secondly, we determined the influence of body weight and age on reproductive success in male Tasmanian devils within group housing. Finally, we used stochastic population models to project population sustainability, loss of genetic diversity and accumulation of inbreeding in intensive housing and group housing over time and explored recommendations to resolve unequal genetic contributions.

Methods

The mating system of Tasmanian devil

Tasmanian devils live on average for 5–6 years [28, 29], and potentially up to 8 years in captivity [30]. Both males and females reach sexual maturity between 1 and 2 years of age, and experience a reproductive life of 3–4 years [31, 32]. The annual breeding season occurs between February and June [33]. Females are polygamous, polyestrous annual breeders, which can produce a maximum of four joeys each year, due to the maximum number of teats [34]. Males are polygamous and have been reported to display mate guarding at dens after copulation [35].

Insurance population management of the Tasmanian devil

The Tasmanian devil insurance metapopulation is managed across a range of breeding facilities including: intensive zoos, group housing enclosures, free-range enclosures, an island population and a fenced peninsula [27]. Breeding recommendations are issued to member institutions annually, indicating which devils should be paired together; not every Tasmanian devil is provided with a breeding opportunity every year. Zoo facilities are intensively managed, where breeding recommendations are most often carried out as single breeding pairs. Group housing (maximum 10 individuals) and free-range facilities (maximum 22 individuals) are less intensively managed. Breeding recommendations in group housing comprise a group of multiple males and females, allowing for mate choice to occur within a selected group of individuals [27]. The island and fenced peninsula populations are monitored annually with population supplementation and removal undertaken as required for genetic and demographic sustainability, as well as source populations for wild release. In sites where breeding can be managed it is done using a traditional species management approach of minimising mean kinship [12] based on pedigree analysis, which is supplemented with molecular data.

In this study, we compared reproductive skew (a measure of unequal genetic contribution) and litter size (offspring survival to weaning, a measure of offspring fitness) between group and intensive housing. Group housing enclosures accommodate approximately 2.67 Tasmanian devils per hectare, with even sex ratios. The enclosures are designed to resemble the natural environment of the Tasmanian devil and provide multiple den sites, crucial for Tasmanian devil reproduction. The Tasmanian devils are housed together all year round, within recommended breeding groups, from December through to November. This allows devils to familiarize themselves with both the enclosure and the other Tasmanian devils prior to breeding season. Genetic parentage of offspring produced in group housing enclosures between 2011 and 2014 was previously determined using a panel of 33 polymorphic microsatellite markers [36]. Parentage data for the 2015 cohort of joeys was determined herein following methods presented in ref [36] where all sexually mature Tasmanian devils residing in the group housing facility during 2015 and all joeys from the 2015 cohort were genotyped using 33 microsatellites and analysed in CERVUS [37] to determine parentage. Intensive facilities vary in enclosure size, with an average of 1–2 devils per enclosure. Females with breeding recommendations are housed independently throughout the year and potential mates are introduced to her enclosure once signs of estrous are evident. A female devil may have multiple males introduced throughout the year (in accordance with estrous cycles) if mating attempts are unsuccessful. The current dataset is limited to those females for which introductions were limited to one male at a time, but includes females that had males introduced to them sequentially. Parentage data for intensive facilities was determined from studbook records. The Zoo and Aquarium Association provide breeding recommendations to the facilities on an annual basis. All breeding recommendations are based on a minimisation of mean kinship strategy using studbook pedigree information.

Intensive (forced monogamy) vs. group housing (mate choice)

To investigate the effect of facility type (group housing or intensive housing) on reproductive skew and litter size we compared these outcomes between facilities

(both defined below). Data from 2011 to 2015 were investigated for both housing types (Table 1). We predicted that group housing would have a higher reproductive skew (a smaller percentage of individuals achieving reproductive success) than intensive housing, as a result of mate choice and competition experienced within communal living. We predicted that females from group housing would have greater litter size than females from intensive housing as a result of the benefits of mate choice. We used generalized linear mixed models (GLMMs) to investigate the effect of facility type. All GLMMs were carried out in R [38] fitted with *glmr* using the R package *lme4* [39]. Male and female models were run separately as forced monogamy and mate-choice can affect sexes differently (for a review see [40]). In total, three models were run as described below.

Reproductive skew

Males and females were analysed separately. Individual reproductive success was a binomial response, where "achieved" was if they produced at least one offspring, and "failed" was if they failed to reproduce. The collective reproductive success and failure rate from each facility represents the reproductive skew of the facility. Along with facility (our predictor of interest), both models included age as a continuous predictor variable and year and individual ID as categorical random factors. We chose to include individual ID to account for repeated measures from individuals across the 5-year study period. In addition, the female reproductive skew model included body weight as a continuous predictable variable. This predictor was not included for the male reproductive skew model, as there were two years of the five where body weight data for both intensive and group housing males were not available.

Litter size

To investigate the impact of facility type on litter size we quantified litter size using a binomial response variable, where the number of events (successes) was the number of offspring produced per litter, and the number of trials was the total number of offspring biologically possible (four due to pouch size [31]). Along with facility (our predictor of interest), age and body weight were included as continuous predictors and year and individual ID were included as categorical random factors.

Male competition

Our male reproductive skew data indicated that males, within group housing, did not exhibit equal reproductive success among the males in a shared enclosure. To test whether reproductive success significantly differed from our null hypothesis (all males sire equal proportions of offspring in an enclosure) we performed a series of multinomial exact tests using the R-package *XNomial* [41]. This approach allows us to examine each enclosure as an independent trial; necessary because the number of males and females varied among enclosures. Over the five-year study

Table 1 Comparison of the reproductive success in Tasmanian devils between two types of housing facilities over a five year period

Facility	Year	Sample size(m:f)	Polygyny[a]	Polyandry[b]	Male reproductive skew[c]	Female reproductive skew[d]	% males reproduced mean (±SD)[e]	% females reproduced mean (±SD)[e]	Litter size mean (±SD)[f]
Group	2011	10:11	0.00	0.00	60.00	63.64	25.00 (5.77)	25.00 (5.77)	2.50 (0.58)
	2012	24:23	40.00	7.70	58.33	43.48	10.00 (4.18)	7.69 (3.43)	2.77 (1.24)
	2013	26:26	8.33	23.08	53.85	50.00	8.33 (4.76)	7.70 (3.50)	2.23 (1.01)
	2014	23:23	10.00	33.33	56.52	59.09	10.00 (4.74)	11.11 (4.76)	2.33 (1.00)
	2015	21:22	37.50	10.00	61.90	50.00	12.50 (4.63)	9.10 (3.07)	3.10 (1.04)
Average		20.8:21	19.17	14.82	58.12	53.24	13.17	12.12	2.59
Intensive	2011	18:17	20.00	NA	44.44	29.41	10.00 (4.92)	8.33 (3.21)	2.58 (0.99)
	2012	17:14	0.00	NA	35.29	21.43	9.09 (3.46)	9.09 (3.46)	2.45 (0.93)
	2013	16:15	16.67	NA	62.50	53.33	16.67 (12.11)	14.29 (5.35)	2.86 (1.07)
	2014[g]	10:8	0.00	NA	50.00	37.50	20.00 (9.31)	20.00 (9.31)	2.80 (1.30)
	2015[g]	13:15	0.00	NA	27.27	40.00	12.50 (4.63)	11.11 (4.17)	2.67 (1.00)
Average		14.8:13.8	7.33	NA	43.9	36.33	13.65	12.56	2.67

[a]Percentage of males that had more than one female mate
[b]Percentage of females that had more than one male mate
[c]Percentage of males that failed to reproduce from the total number of males with breeding recommendations
[d]Percentage of females that failed to reproduce from the total number of females with breeding recommendations
[e]Average individual reproductive contribution (number of joeys produced as a proportion of the total number of joeys produced in that yearly cohort)
[f]Average litter size value obtained only from females that reproduced during this study
[g]In these two years, breeding recommendations were preferentially giving to group housing facilities due to capacity restrictions in the intensive facilities in the insurance population ([52])
Group housing facilities provide an opportunity for mate choice, and intensive housing facilities require forced monogamy

period we had 26 group housing enclosures (*n-trials = 26*). A substantial proportion of enclosures were significantly different from our null hypothesis (see Results).

To further understand what factors may influence reproductive variance we investigated whether standardized body weight determined male reproductive success in group housing enclosures using a GLMM. Our model represented reproductive success as a binomial response, where an individual achieved a success event if they sired at least one offspring, and achieved a fail event if they sired no offspring. The captive environment of group housing violates certain assumptions for male competition. Males exist in closed populations, where each individual male is in competition with only a subset of males, which can vary in body weight range across enclosures, and across years. We wanted to investigate whether male competition to be the superior male was a result of being the largest male per enclosure (each male is compared to the remaining males in said enclosure), or alternatively, if superior males had a body weight threshold (regardless of body weight ranking per enclosure, all individuals below a certain body weight are generally inferior males) (for a review on male body weight and reproductive success in invertebrates, reptiles, birds and mammals see [24]). To investigate this question our predictor of interest was standardised male body weight within enclosure (denoted "s.bodyweight") for the three years body weight data was available, calculated as the difference between a males individual body weight and the mean body weight for all males within the enclosure (i.e. $s.bodyweight = bodyweight - bodyweight_{enclosure\ mean}$). Age and s.bodyweight were included as our predictors of interest, along with year and individual ID as categorical random factors.

All global models, for all our GLMMs, were standardised to facilitate comparison of parameter estimates across models, using the *arm* package [42] in R. Model selection proceeded under information theory (following ref [44]). From each standardised global model we created a complete subset of models using the *MuMIn* package [43] in R. Each submodel was ranked using the Akaike's information criterion (AIC_C), and conditional model averaging was used to take all models that fell within 2 AIC_C of the highest ranked model (see Additional file 1: Tables S2-S5). Inference was based on standardised effect sizes, their standard errors, and the relative importance (RI) scores for each predictor [44].

Population growth, genetic diversity and inbreeding modeling: Intensive housing (forced monogamy) vs. group housing (mate choice)

To investigate the long-term population differences between intensive housing and group housing we used stochastic population models to project population growth (or sustainability at carrying capacity), gene diversity and inbreeding accumulation over time using VORTEX v10 [45, 46]; all input parameters are shown in Additional file 1: Table S1. Models were run for 50 years, as this is the intended length of the Tasmanian devil insurance population [47], and a general milestone applied to insurance populations. The initial population size and long-term carrying capacity were equal between the intensive housing model and the group housing model (to allow comparisons over time). The carrying capacity was chosen to reflect a breeding age distribution similar to that maintained by conservation breeding programs broadly, in general terms more younger individuals than older animals and equal sex ratio. Female reproductive parameters were determined from our GLMM results, as opposed to directly applying our empirical data. We did this for two reasons; 1) female reproductive success was not influenced by facility type, and using our modeled results indicated for a single value for females across both management strategies, and 2) the modeling data summarises our dataset as a whole, providing a more accurate estimate of mean effects than data from any given subset (such as year). Mortality rates were set as equal between facilities, to enable strict comparison of reproductive processes alone, and were derived from direct census data from the Tasmanian devil insurance population. As age was found to be a significant predictor of reproductive success for female Tasmanian devils [36], the reproductive rate for females was entered as a function of age (Additional file 1: Table S1). For a baseline model, male reproductive rate had a 0% skew in both facilities (i.e. 100% of the males were contributing to the breeding pool), with all remaining parameters equal excluding mating opportunities (Additional file 1: Table S1), as this reflects the key difference between group housing and intensive housing. All models were run for 1000 iterations and average results reported.

To investigate how reproductive skews in intensive and group housing influences population growth (or sustainability at carrying capacity), gene diversity and inbreeding accumulation we ran a series of simulation models with gradually increasing reproductive skew. Eight models were run for each enclosure type, whereby reproductive skew increased at 10% increments from 0 to 70% (e.g. a model run with a 70% male reproductive skew operates with only 30% of the male population contributing to the breeding pool in a given year).

Finally, we investigated the impact of transfers between our two management types, in the face of average reproductive skews. All parameters were set to those listed in Additional file 1: Table S1, with the exception of male reproductive skews being set to the average observed percent for each enclosure type (58.12% for group housing and 43.90% for intensive housing). Eleven models were run; a

baseline model with the aforementioned male reproductive skews for each facility and zero transfers; transferring 1, 3 or 5 males every year between the two facilities; transferring 1, 3, or 5 females every year between the two facilities; and transferring 3 or 5 males or females every 3 or 5 years between the two facilities. Male and female transfers were investigated separately because females were predicted to have a greater probability than males of contributing to the breeding pool in the presence of male reproductive skews. Our models were built so that an individual could only be transferred to its non-origin facility, and could not be transferred back in subsequent years. Raw data for the analyses presented in this paper are available in Additional file 2 (females) and Additional file 3 (males).

Results

In total, empirical data from five mating seasons were analyzed (2011 to 2015) representing 69 breeding recommendations within intensive enclosures, of which 63.67% of females and 56.10% of males were successful (produced at least 1 offspring); and 105 breeding recommendations within group housing enclosures, of which 46.76% of females and 41.88% of males were successful. In group housing 19.17% of successful males were polygynous and 14.82% of successful females polyandrous (Table 1). Females did not have more than two mates per season, and only one male had three mates in a single breeding season, with the remaining polygynous males all having two mates. There were three occurrences of polygyny within the intensive facilities, when one male was given the opportunity to reproduce with two females on separate occasions (7.33% of mated males).

Reproductive skew

For males, reproductive skew ranged from 53.85% to 61.90% in group housing and 27.27% to 62.50% in intensive housing (Table 1). Our models provided poor support for an effect of group housing on male reproductive skew (Table 2). Female reproductive skew ranged from 43.48% to 63.64% in group housing and 21.43% to 53.33% in intensive housing (Table 2). Modeling female reproductive skew showed that age was the most accurate predictor of female reproductive success (Table 2), with a strong negative effect of age on reproductive output. Enclosure type (group or intensive) and body weight were present in models <2AIC of the top model, but were poorly supported as predictors of female reproductive skew (low RI and imprecise estimates with high standard error; Table 2).

Litter size

There was no significant difference in the number of offspring produced in the group housing enclosures (2.60 ± 1.07 SD joeys/female) when compared to the intensive enclosures (2.64 ± 0.99 SD joeys/female) (Tables 1 and 2). Age appeared within 2 AIC of the top model for litter size, although evidence for this effect was poor (very low RI and high error; Table 2).

Male competition

Of the 26 group housing enclosures, each enclosure had a minimum of one female reproduce. We found statistically significant deviations from equal siring success for males in 11 of the 26 group enclosures (Table 3). This effect was observed at a higher frequency when 4 joeys (or more) were produced per an enclosure, occurring in 11 out of 16 trials (i.e. a statistically significant deviation from uniform representation at $\alpha = 0.05$ was seen in 68.75% of enclosures where at least 4 joeys were produced). In 10 enclosures where <4 joeys were produced, none deviated significantly from the null hypothesis of uniform representation (Table 3). Trials with low female reproductive success (small number of total joeys produced) likely limits our ability to detect male competition.

After model averaging, standardised body weight appeared in the top model for male Tasmanian devils in group housing, showing a strong positive effect of standardised weight on reproductive success (Table 2). Standard error was small (confidence intervals do not encompass zero) and the relative importance value was high (1.00; Table 2). Larger males within an enclosure were significantly more likely to achieve reproductive success than smaller males. Age appeared in the top model or a model within 2 AIC of the top model for male Tasmanian devil in group housing, but was poorly supported (Table 2).

Population growth, genetic diversity and inbreeding modeling: Intensive (forced monogamy) vs. group housing (mate choice)

Models, using Vortex, showed that after 50 years, in the absence of male reproductive skew (i.e. 100% of the males were contributing to the breeding population), population growth, gene diversity and inbreeding accumulation were very similar between group housing and intensive housing. The population size fluctuated mildly throughout the 50 year time period for both populations; group housing averaged 88.14 Tasmanian devils after 50 years, and intensive housing averaged 88.06 Tasmanian devils after 50 years. Gene diversity was similar between the two facilities, with group housing predicted to maintain 84.95% gene diversity and intensive housing predicted to maintain 85.07% gene diversity. Inbreeding coefficients were also similar, with group housing predicted to have a mean inbreeding coefficient of 0.13 after 50 years and intensive housing predicted to have a mean inbreeding coefficient of 0.14 after 50 years.

Table 2 Summary of standardised predictors and their relative importance after conditional averaging of top models (all models within $2AIC_C$) (see methods for details on predictors in each global model)

Response variable	Predictor variables[a]	Coefficient	SE[b]	CI 95% U	CI 95% L	RI[c]
Male reproductive skew	Group housing	−0.65	0.39	0.11	−1.41	0.61
	Age	−0.47	0.35	0.22	−1.16	0.46
Female reproductive skew	**Age**	**−2.47**	**0.90**	**−0.71**	**−4.23**	**1.00**
	Group housing	−0.53	0.61	0.67	−1.73	0.27
	Body weight	−0.22	0.54	0.84	−1.28	0.20
Female litter size	**Age**	**−0.12**	**0.05**	**−0.02**	**−0.22**	**0.29**
Male reproductive success[d]	**Standardised weight**	**1.76**	**0.61**	**2.96**	**0.56**	**1.00**
	Age	−0.46	0.53	0.58	−1.50	0.32

All bold trials indicate enclosures that significantly deviated from equal siring success
[a]Standardised predictors to a mean of 0 and a standard deviation of 0.5; all bold predictor variables have confidence intervals that do not include zero
[b]SE; standard error
[c]RI; relative importance
[d]Model uses data from group housing and does not include data from intensive housing

As male reproductive skew increased, we saw a decrease in genetic diversity and an increase in inbreeding accumulation, over 50 years, in both enclosure types (Fig. 1). Loss of gene diversity and inbreeding accumulation was most prominent for intensive enclosures when male reproductive skew was greater than 60% (i.e. less than 40% of the males were successfully reproducing). The results most reflective of the Tasmanian devil insurance population are displayed in Fig. 2. Group housing had a male reproductive skew of 58.12% and intensive housing had a male reproductive skew of 43.90%. Despite minimal differences existing between the two facilities

Table 3 Results of multinomial tests for equal siring success among males within group housing enclosures of Tasmanian devils

Trial	Number of Males	Year	Male #1*†	Male #2*†	Male #3*†	Male #4*†	Male #5*†	Number of Joeys	P-value
1	2	2011	2	0				2	0.5
2	3	2013	1	0	0			1	1
3	3	2012	2	0	0			2	0.33
4	**3**	**2013**	**4**	**0**	**0**			**4**	**0.04**
5	**3**	**2012**	**5**	**0**	**0**			**5**	**0.01**
6	**3**	**2012**	**6**	**3**	**0**			**9**	**0.04**
7	4	2014	2	0	0	0		2	0.25
8	4	2014	2	0	0	0		2	0.25
9	4	2011	3	0	0	0		3	0.06
10	4	2013	2	1	0	0		3	0.63
11	4	2013	2	1	0	0		3	0.63
12	4	2014	3	0	0	0		3	0.06
13	4	2014	2	1	0	0		3	0.63
14	**4**	**2015**	**4**	**0**	**0**	**0**		**4**	**0.02**
15	4	2011	3	2	0	0		5	0.18
16	4	2013	3	2	0	0		5	0.18
17	4	2013	4	1	0	0		5	0.06
18	**4**	**2012**	**4**	**3**	**0**	**0**		**7**	**0.05**
19	**4**	**2015**	**5**	**2**	**0**	**0**		**7**	**0.02**
20	4	2012	4	3	1	0		8	0.2
21	**4**	**2013**	**5**	**3**	**0**	**0**		**8**	**0.02**
22	**4**	**2015**	**4**	**4**	**0**	**0**		**8**	**0.02**
23	**4**	**2015**	**6**	**2**	**0**	**0**		**8**	**0.01**
24	**5**	**2015**	**4**	**0**	**0**	**0**	**0**	**4**	**0.01**
25	**5**	**2012**	**5**	**0**	**0**	**0**	**0**	**5**	**0**
26	5	2014	4	3	2	1	1	11	0.37

*The number of males within an enclosure ranged between two and five. When an enclosure did not contain all possible five males, the absence is denoted with grey shading
†Number of joeys produced by individual male
All bold trials indicate enclosures that significantly deviated from equal siring success

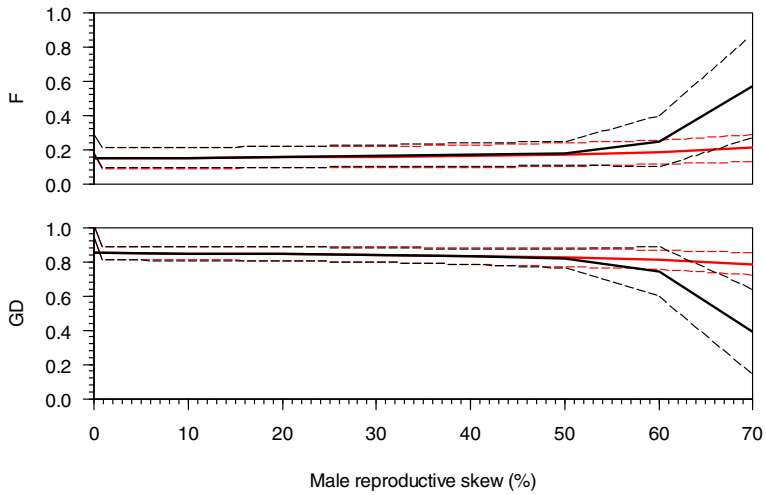

Fig. 1 Predicted inbreeding accumulation (F; top panel) and genetic diversity (GD; bottom panel) after 50 years, across a male reproductive skew gradient in two isolated captive breeding facilities for the Tasmanian devil. Both facilities originated from 40 founders of even sex ratios, and had a carrying capacity of 100. Solid and dashed red lines represent a group enclosure facility (mean (solid line) ± SD (dashed lines), respectively) and the black lines represent an intensive enclosure facility (mean (solid line) ± SD (dashed lines), respectively). See Additional file 1: Table S1 for detailed Vortex parameters and methods section for rationale

under 0% male reproductive skew, observed levels of skew reveal a pattern whereby intensive housing accumulated less inbreeding and maintained a degree of higher gene diversity over the 50 year period than group housing (Fig. 2).

Simulated transfers of both male and female Tasmanian devils between group housing and intensive housing led to predicted increases in gene diversity and decreases in inbreeding accumulation. The change in gene diversity (increase) and inbreeding (decrease) was greatest when comparing the predicted outcome between zero transfers and one (male or female) annual transfer (Table 4). It should be noted that transferring females gave consistently greater increases in gene diversity and greater decreases in inbreeding accumulation relative to transferring males (Table 4).

Discussion

For some critically endangered species, such as the giant panda [13] and cheetah [21], providing individuals with the opportunity for mate choice has led to successful

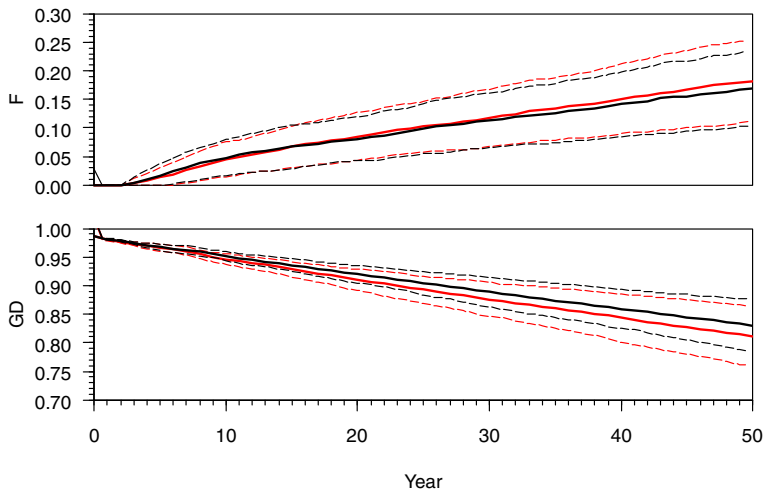

Fig. 2 Predicted inbreeding accumulation (F; top panel) and genetic diversity (GD; bottom panel) after 50 years in two isolated captive breeding facilities for the Tasmanian devil. Both facilities originated from 40 founders of even sex ratios, and had a carrying capacity of 100. Solid and dashed red lines represent a group enclosure facility (mean (solid line) ± SD (dashed lines), respectively) and the black lines represent an intensive enclosure facility (mean (solid line) ± SD (dashed lines), respectively). See Additional file 1: Table S1 for detailed Vortex parameters and methods section for rationale

Table 4 Predicted genetic diversity (GD) retention and inbreeding (F) accumulation in group and intensive housing facilities for the endangered Tasmanian devil, after 50 years, given different numbers of individuals transferred between facilities

Ntransfer[a]	Frequency (Years)	Sex	Group GD	Intensive GD	Group F	Intensive F
0	NA	NA	0.81	0.83	0.18	0.17
1	1	M	0.87	0.88	0.12	0.12
1	1	F	0.88	0.88	0.11	0.11
3	1	M	0.88	0.88	0.10	0.10
3	1	F	0.89	0.89	0.10	0.10
3	3	M	0.87	0.88	0.11	0.12
3	3	F	0.88	0.88	0.11	0.11
5	1	M	0.89	0.89	0.10	0.10
5	1	F	0.89	0.89	0.09	0.10
5	5	M	0.88	0.88	0.11	0.11
5	5	F	0.88	0.88	0.11	0.11

[a]number of transfers between group housing and intensive housing facilities

reproduction in captive programs. However, here we have shown that an understanding of the impact of different housing on retention of genetic diversity is essential to the long-term management of any insurance population. As the global biodiversity crisis deepens and more species are under threat, conservation breeding programs and insurance populations are seen as viable solutions to species survival. Severe reproductive skews during the establishment of an insurance population will have long spanning consequences. These skews can arise as a result of forced monogamy, mate incompatibilities, intrasexual competition, or a combination of these. Teasing apart the mechanisms causing reproductive skews, and their consequences, in small populations is crucial for conservation management, particularly for genetically depauperate species such as Tasmanian devils [48]. Ours is one of only a handful of studies that examines these effects empirically in a long-running, intensively managed population. We show that genetic diversity in the Tasmanian devil insurance metapopulation is retained more effectively in intensive housing (forced monogamy) when compared to group (max 10 individuals) housing (mate choice). Furthermore, we show that purported benefits of mate choice, such as increased offspring survival, were not realized as both group and intensively housed animals showed similar litter sizes at weaning. This finding is in line with other work across the entire Tasmanian devil insurance population that showed intensive and group housing facilities produced on average 2.51 ± 0.23 joeys/female compared with larger free-range enclosures (3.05 ± 0.41 joeys/female) and Maria Island (3.10 ± 0.21 joeys/female) [27].

As part of the insurance metapopulation strategy Tasmanian devils have been housed in group scenarios to provide better mate choice and/or competition as well as maintain individuals in a more "wild-type" environment. The agile antechinus (*Antechinus agilis*), from the same Dasyurid family as the Tasmanian devil, has been shown to preferentially mate and produce young with genetically dissimilar males when provided with a range of potential mates [49, 50]. Chemosensory cues have been shown to play an influential role in this antechinus mate-choice process [49]. Similar to the antechinus, the Tasmanian devil has been observed to regularly scent mark [51]. The purpose of devil scent marking has not been investigated, but it is plausible that it plays a similar role in territory marking and may influence female mate choice. In theory, when provided with mate choice opportunities, female Tasmanian devils may favour dominant males (if they have engaged in more scent marking) or the most genetically diverse male (potentially determined via olfactory cues). However, the correlation between neutral diversity and male reproductive success has been previously investigated in group housing facilities with no significant influence being detected [36].

Providing Tasmanian devils with mate choice opportunities has resulted in a reproductive skew in the insurance population. Only 41.88% of all possible males have contributed genetically over the five-year period. Further, there was no fitness benefit in the productivity of offspring between group and intensive housing. The Tasmanian devil insurance metapopulation has been very successful to date with reproductive goals surpassed annually [27] and demographic sustainability achieved. However, allowing group housing for the purpose of mate choice in this species is not an optimal long-term genetic management strategy, as reproductive skew will hinder the maintenance of genetic diversity.

Due to the short reproductive life (1–3 years) of Tasmanian devils, the unknown parentage of offspring produced in group housing has meant annual breeding recommendations are issued before the mean kinship of

any given year's offspring can be determined through genetic analyses [52]. This is because annual breeding recommendations are issued in September each year to permit the transfer of devils before the heat of the austral summer and breeding season the following March. Joeys wean from September through to December with parentage analysis only able to be completed by the following January/February. Whilst subtle departures from equal breeding success are expected to occur naturally in group enclosures (and in the wild), the results presented herein suggest male competition within enclosures creates significantly unequal reproductive success. Of the 26 enclosures examined, 11 had one male siring a significantly greater number of offspring (Table 3). In addition, five of these 11 enclosures had only one male reproducing and the remaining six enclosures had only two males reproducing. This means that each year as many as 50% - 80% of males housed in group enclosures and provided with the opportunity to breed produce no offspring. This has led to a reproductive skew in the insurance population potentially affecting the long-term retention of genetic diversity. Fortunately group housing has only been used in the insurance metapopulation since 2011 and so knowledge of this reproductive skew can now be accounted for in future breeding recommendations.

To better understand why only a small portion of available males were siring offspring we investigated the role of body weight on male reproductive success. Regardless of an individual's age we found that large males are most likely to contribute the greatest proportion of joeys to the annual joey cohort. As the breeding yards are adjusted each year, we suggest that predetermined residency (or territory) may not be the greatest driver of reproductive success, but rather male body size. For many insurance populations experiencing difficulties with maintaining equal genetic representation, unavoidable overrepresentation of more manageable breeding pairs can play a role (e.g. mate aggression in the black rhinoceros (*Diceros bicornis*) inadvertently led to more frequent breeding opportunities between more timid or adapted individuals [53]). In other endangered species that experience reproductive skews and pair incompatibilities, such as pygmy rabbits (*Brachylagus idahoensis*) and clouded leopards (*Neofelis nebulosa*), long-term exposure to a genetically desirable breeding partner, prior to breeding season, increased reproductive success in both species [16, 54]. Reproductive dominance in males has been observed in the endangered gopher tortoise (*Gopherus polyphemus*) where larger males achieve the greatest reproductive output annually in a heavily monitored rewilding site [55]. In the Tasmanian devil, the annual breeding recommendations for group housing enclosures provide for a staggered age structure, as housing individuals of the same age together for breeding may lead to over-aggressive behaviours (DPIPWE/ZAA 2013; STDP *pers. comm.*). Given body weight, rather than age, is a greater determinant of reproductive success in group housed male Tasmanian devils, different management strategies will be required to balance genetic representation in the future. For male Tasmanian devils within intensive facilities, both age and body weight had negligible effect on individual reproductive success. Further analysis into the potential reproductive skew in free-range enclosures (1 devil/ha) and at the island site (0.5–0.8 devils/ha) will provide a better understanding of the interplay of weight and density on the reproductive success of male Tasmanian devils.

The overarching aim of the Tasmanian devil insurance population is to maintain at least 95% of wild-sourced genetic diversity for 50 years [47]. By modelling varying reproductive success of male Tasmanian devils in both group and intensive housing we were able to assess how these differing approaches would sustain population size, retain gene diversity and accumulate inbreeding over the 50 years. There was a gradual increase of inbreeding accumulation in group housing (relative to intensive) and gradual decrease in gene diversity in group housing (relative to intensive) over 50 years (Fig. 2). However, as the Tasmanian devil insurance population operates as a metapopulation we modelled the impact transfers would have on the gene retention and inbreeding accumulation under differing male reproductive skews. In the face of "average" male reproductive skews within both facilities, the transfer of a single male or female Tasmanian devil annually restored a significant degree of genetic diversity to the population and greatly decreased the accumulation of inbreeding within the population (Table 4). This demonstrates the value and necessity of cooperative management for insurance populations.

Conclusions

The concept of group housing in conservation breeding programs is becoming increasingly topical, providing many behavioural and welfare advantages, in addition for mate choice opportunities. However, management teams should be cautious of using solely a group housing approach, as this can potentially obstruct the long-term genetic maintenance goal for the species. Captive breeding programs traditionally aim to maintain diversity by identifying the breeding combinations that would maximise genetic diversity of the population, and then housing those breeders together, a type of forced monogamy, regardless of species life history. Our study is one of the few studies to have tested the immediate and long-term consequences of providing mate choice opportunities in an insurance program. We found that the purported benefits of these mate choice opportunities were not

realised in Tasmanian devils. Larger litter sizes did not occur in group housing, and there was a high degree of reproductive skew detected in group enclosures raising serious concerns about maintenance of genetic diversity and accumulation of inbreeding. Larger males were significantly more likely to achieve reproductive success in group enclosures compared to smaller males, suggesting intrasexual competition can influence group housing outcomes. Using computational simulations, our population projections reinforced these conclusions, and showed that negative genetic effects can be mitigated through frequent transfers among sites. Group housing during the breeding season is appropriate for many species of conservation concern for welfare and other reasons; we show that acute awareness of reproductive skew, and what is the potential causative for this skew, is essential to the effective use of group housing in conservation breeding programs.

Additional files

Additional file 1: Table S1. Vortex parameters for the Tasmanian devil insurance population across two housing types; group housing and intensive housing. **Table S2.** Top model set (top $2AIC_c$) of generalised linear mixed models for male reproductive skew. **Table S3.** Top model set (top $2AIC_c$) of generalised linear mixed models for female reproductive skew. **Table S4.** Top model set (top $2AIC_c$) of generalised linear mixed models for litter size. **Table S5.** Top model set (top $2AIC_c$) of generalised linear mixed models for group housing male reproductive success. (DOCX 16 kb)

Additional file 2: Raw Data Female Tasmanian Devils. (CSV 4 kb)

Additional file 3: Raw Data Male Tasmanian Devils. (CSV 5 kb)

Abbreviations

AIC: Akaike's Information Criterion; DFT1: Devil Facial Tumour 1; DFT2: Devil Facial Tumour 2; F: Inbreeding coefficient; GD: Genetic Diversity; GLMM: Generalised Linear Mixed Model; RI: Relative Importance; SD: Standard Deviation; STDP: Save the Tasmanian Devil Program; ZAA: Zoo and Aquarium Association

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Availability of data and materials

All data generated or analysed during this study are included in this published article [and its Additional files].

Authors' contributions

RG, CEG, KB and CJH designed the study; data analysis was performed by all authors; the article was drafted and tables and graphs were prepared by RG; all authors revised the article and all authors approved the final version.

Ethics approval

Sampling for this study occurred under approval from University of Sydney Ethics Committee #2014/550.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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References

1. Conde DA, Flesness N, Colchero F, Jones OR, Scheuerlein A. An emerging role of zoos to conserve biodiversity. Science. 2011;331:1390–1.
2. Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks TM, Butchart SHM, Carpenter KE, Chanson J, Collen B, Cox NA, et al. The impact of conservation on the status of the world's vertebrates. Science. 2010;330:1503–9.
3. Toone WD, Wallace MP. The extinction in the wild and reintroduction of the California condor (*Gymnogyps californianus*). In: Olney PJS, Mace GM, Feistner ATC editors. Creative Conservation. Springer Dordrecht; 1994. p. 411–419
4. Kierulff M, Ruiz-Miranda C, Oliveira PP, Beck B, Martins A, Dietz J, Rambaldi D, Baker A. The golden lion tamarin *Leontopithecus rosalia*: a conservation success story. Int Zoo Yearb. 2012;46(1):36–45.
5. Santymire RM, Livieri TM, Branvold-Faber H, Marinari PE. The Black-Footed Ferret: On the Brink of Recovery? In: Holt WV, Brown JL, Comizzoli P, editors. Reproductive Sciences in Animal Conservation: Progress and Prospects. New York, NY: Springer New York; 2014. p. 119–34.
6. Ebenhard T. Conservation breeding as a tool for saving animal species from extinction. Trends Ecol Evol. 1995;10(11):438–43.
7. Ralls K, Ballou J. Captive breeding programs for populations with a small number of founders. Trends Ecol Evol. 1986;1(1):19–22.
8. Fa JE, Funk SM. O'Connell D. Zoo Conservation Biology. UK: Cambridge University Press; 2011.
9. Frankham R, Ballou JD, Briscoe DA. Introduction to conservation genetics (2nd edition), 2nd edition edn. Cambridge: UK Cambridge University Press; 2010.
10. Lacy RC. Analysis of founder representation in pedigrees: founder equivalents and founder genome equivalents. Zoo Biol. 1989;8:111–23.
11. Ballou JD, Lacy RC. Identifying genetically important individuals for management of genetic diversity in pedigreed populations. In: Ballou JD, Gilpin M, Foose TJ, editors. Population management for survival and recovery. New York, NY: Columbia University Press; 1995. p. 76–111.
12. Ballou JD, Lees CM, Faust LJ, Long S, Lynch C, Bingaman-Lackey L, Foose TJ. Demographic and genetic management of captive populations. Wild mammals in captivity. Chicago, London: University of Chicago; 2010.
13. Martin-Wintle MS, Shepherdson D, Zhang G, Zhang H, Li D, Zhou X, Li R, Swaisgood RR. Free mate choice enhances conservation breeding in the endangered giant panda. Nat Commun. 2015;6:10125.
14. Asa CS, Traylor-Holzer K, Lacy RC. Can conservation-breeding programmes be improved by incorporating mate choice? Int Zoo Yearb. 2011;45(1):203–12.
15. Schulte-Hostedde AI, Mastromonaco GF. Integrating evolution in the management of captive zoo populations. Evol Appl. 2015;8(5):413–22.
16. Yamada JK, Durrant BS. Reproductive parameters of clouded leopards (*Neofelis nebulosa*). Zoo Biol. 1989;8:223–31.

17. Fuerst P, Maruyama T. Considerations on the conservation of alleles and of genic heterozygosity in small managed populations. Zoo Biology. 1986;5(2): 171–9.
18. Lacy R. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population subdivision. Conserv Biol. 1987;1(2):143–58.
19. Neff B, Pitcher T. Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. Mol Ecol. 2005;14:19–38.
20. Ihle M, Kempenaers B, Forstmeier W. Fitness benefits of mate choice for compatibility in a socially monogamous species. PLoS Biol. 2015;13(9): e1002248.
21. Batkay D. Mate selection preferences of captive female cheetahs (*Acinonyx jubatus*): York University; 2005.
22. Miller KA, Nelson NJ, Smith HG, Moore JA. How do reproductive skew and founder group size affect genetic diversity in reintroduced populations? Mol Ecol. 2009;18(18):3792–802.
23. Kokko H, Rankin DJ. Lonely hearts or sex in the city? Density-dependent effects in mating systems. Philos Trans Royal Soc B. 2006;361(1466):319–34.
24. Hunt J, Breuker CJ, Sadowski JA, Moore AJ. Male-male competition, female mate choice and their interaction: determining total sexual selection. J Evol Biol. 2009;22(1):13–26.
25. Loh R, Bergfeld J, Hayes D, O'Hara A, Pyecroft S, Raidal S. The pathology of devil facial tumor disease (DFTD) in Tasmanian devils (*Sarcophilus harrisii*). Vet Pathol. 2006;43(6):890–5.
26. Pye RJ, Pemberton D, Tovar C, Tubio JMC, Dunn KA, Fox S, Darby J, Hayes D, Knowles GW, Kreiss A, et al. A second transmissible cancer in Tasmanian devils. Proc Natl Acad Sci U S A. 2016;113(2):374–9.
27. Hogg CJ, Lee AV, Srb C, Hibbard C. Metapopulation management of an endangered species with limited genetic diversity in the presence of disease: the Tasmanian devil *Sarcophilus harrisii*. Int Zoo Yearb. 2016;51:1–17.
28. Guiler ER. Observations on the Tasmanian devil, *Sarcophilus harrisii* (Marsupialia: Dasyuridae). I. Numbers, home range, movements, and food in two populations. Aust J Zool. 1970;18:49–62.
29. Guiler ER. Observations on the Tasmanian devil, *Sarcophilus harrisii* (Dasyuridae: Marsupialia) at Granville harbour, 1966-75. Pap Proc R Soc Tasmania. 1978;112:161–88.
30. Srb C: Tasmanian devil studbook, Healesville sanctuary on behalf of the Zoo and Aquarium Association. 2016.
31. Guiler E. Observations on the Tasmanian devil, *Sarcophilus harrisii* (Marsupialia: Dasyuridae) II. Reproduction, breeding and growth of pouch young. Aust J Zool. 1970;18(1):63–70.
32. Keeley T, O'Brien JK, Fanson BG, Masters K, McGreevy PD. The reproductive cycle of the Tasmanian devil (*Sarcophilus harrisii*) and factors associated with reproductive success in captivity. Gen Comp Endocrinol. 2012;176(2):182–91.
33. Keeley T, Russell T, Carmody K, Kirk G, Eastley T, Britt-Lewis A, Post M, Burridge M, Eccleston S, Faulkner T, et al. Seasonality and breeding success of captive and wild Tasmanian devils (*Sarcophilus harrisii*). Theriogenology. 2017;95:33–41.
34. Hughes RL. Reproduction in the Tasmanian devil *Sarcophilus harrisii* (Dasyuridae, Marsupialia). In: Archer M, editor. Carnivorous Marsupials. Sydney: Surrey Beatty and Sons; 1982. p. 49–63.
35. Pemberton D. Social organisation and behaviour of the Tasmanian devil, *Sarcophilus harrisii*: University of Tasmania; 1990.
36. Gooley R, Hogg C, Belov K, Grueber C. No evidence of inbreeding depression in a Tasmanian devil insurance population despite significant variation in inbreeding. Sci Rep. 2017;7(1):1830
37. Kalinowski S, Taper M, Marshall T. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol. 2007;16(5):1099–106.
38. R Core Team: R: A language and environment for statistical computing. Vienna. Available: http://www.r-project.org/. 2015.
39. Bates D, Maechler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. J Stat Softw. 2015;67(1):1–48.
40. Edward DA. The description of mate choice. Behav Ecol. 2014;26(2):301–10.
41. Edwards K, Walker S, Dunham A, Pilgrim M, Okita-Ouma B, Shultz S. Low birth rates and reproductive skew limit the viability of Europe's captive eastern black rhinoceros, *Diceros bicornis michaeli*. Biodivers Conserv. 2015; 24:2831–52.
42. Gelman A, Su Y-S, Yajima M, Hill J, Pittau MG, Kerman J, Zheng T, Dorie V: arm: Data analysis using regression and multilevel/hierarchical models. http://CRAN.R-project.org/package=arm 2015.
43. Bartoń K: MuMIn: Multi-model inference. https://CRAN.R-project.org/package=MuMIn 2016.
44. Grueber CE, Nakagawa S, Laws RJ, Jamieson IG. Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol. 2011;24(4):699–711.
45. Lacy RC. VORTEX: a computer simulation model for population viability analysis. Wildl Res. 1993;20:45–65.
46. Lacy RC. Structure of the VORTEX simulation model for population viability analysis. Ecol Bull. 2000;48:191–203.
47. CBSG. Tasmanian devil PHVA final report. In: IUCN/SSC Conservation Breeding Specialist Group: Apple Valley, MN; 2008.
48. Miller W, Hayes VM, Ratan A, Petersen DC, Wittekindt NE, Miller J, Walenz B, Knight J, Qi J, Zhao FQ, et al. Genetic diversity and population structure of the endangered marsupial *Sarcophilus harrisii* (Tasmanian devil). Proc Natl Acad Sci U S A. 2012;109(45):18625–5.
49. Parrott ML, Ward SJ, Temple-Smith PD. Olfactory cues, genetic relatedness and female mate choice in the agile antechinus (*Antechinus agilis*). Behav Ecol Sociobiol. 2007;61(7):1075–9.
50. Parrott ML, Ward SJ, Temple-Smith PD, Selwood L. Females choose mates based on genetic relatedness in a small Dasyurid marsupial, the agile antechinus (*Antechinus agilis*). PLoS One. 2015;10(4):e0122381.
51. Lazenby BT, Dickman CR. Patterns of detection and capture are associated with cohabiting predators and prey. PLoS One. 2013;8(4):e59846.
52. Hogg CJ, Ivy JA, Srb C, Hockley J, Lees C. Influence of genetic provenance and birth origin on productivity of the Tasmanian devil insurance population. Conserv Genet. 2015;16:1465–73.
53. Edwards KL, Walker SL, Dunham AE, Pilgrim M, Okita-Ouma B, Shultz S. Low birth rates and reproductive skew limit the viability of Europe's captive eastern black rhinoceros, *Diceros bicornis michaeli*. Biodivers Conserv. 2015; 24(11):2831–52.
54. Martin MS, Shepherdson DJ. Role of familiarity and preference in reproductive success in ex situ breeding programs. Conserv Biol. 2012;26(4): 649–56.
55. Tuberville TD, Norton TM, Waffa BJ, Hagen C, Glenn TC. Mating system in a gopher tortoise population established through multiple translocations: apparent advantage of prior residence. Biol Conserv. 2011;144(1):175–83.