Pedigree analysis reveals a generational decline in reproductive success of captive Tasmanian devil (Sarcophilus harrisii): implications for captive management of threatened species

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Received November 20, 2016; First decision January 4, 2017; Accepted March 24, 2017.

Corresponding Editor: Dr. Oliver Ryder

Abstract

Captive breeding programs are an increasingly popular tool to augment the conservation of threatened wild populations. Many programs keep detailed pedigrees, which are used to prescribe breeding targets to meet demographic and genetic goals. Annual breeding targets are based on previous productivity, but do not account for changes in reproductive success that may occur over generations in captivity and which may impair the ability of a program to meet its goals. We utilize a large studbook from the Tasmanian devil (Sarcophilus harrisii) captive breeding program to investigate biological, genetic, and environmental factors that affect variation in reproductive success among individuals and over generations of captive breeding. Reproductive success declined with increasing generations in captivity: wild-born females had a 56.5% chance of producing a litter compared to a 2.8% chance for generation 5 captive-born females ($N = 182$) and when they did, wild-born females produced more offspring (3.1 joeys, 95% CI: 2.76–3.38, compared to 2.7 joeys, 95% CI: 2.55–2.90, in captive-born females [$N = 105$]). Reproductive success also declined as dam age at first breeding increased. Our results reveal a conflict with the widely cited conservation strategy to limit opportunity for selection by extending generation length through delaying reproduction, as captive breeding programs that delay female breeding with this goal in mind risk reduced productivity. Our data demonstrate the benefit of pedigree analysis to identify biological processes that reveal crucial trade-offs with conservation best-practice.

Subject area: Conservation genetics and biodiversity

Key words: adaptation to captivity, captive breeding, inbreeding, reproduction, senescence

Introduction

The world is facing an extinction crisis, with 26% of mammalian species threatened globally (IUCN 2014). In response, conservation management is becoming increasingly intensive, utilizing translocations, reintroductions, metapopulation management, and captive breeding to support wild populations (Pritchard et al. 2012; Seddon
The International Union for the Conservation of Nature (IUCN) has recognized the value of breeding threatened species in captivity until reintroductions to the wild are possible (Conde et al. 2011), and so reintroduction is a stated goal of many “insurance populations” today (Conway 2011). *Ex situ* management (i.e., captive breeding for reintroduction) aims to minimize genetic diversity loss, inbreeding and adaptation to captivity, in order to retain founder diversity, avoid inbreeding depression, and maximize evolutionary potential (Ballou et al. 2010). Quantitative goals are used, such as retaining over 90% of wild-sourced genetic diversity over 100 years (Ballou et al. 2010). Demographically, programs aim to rapidly increase population size to avoid extinction and maintain reliable reproduction (Frankham et al. 2004).

The World Zoo and Aquarium Conservation Strategy recommends the use of highly controlled breeding strategies to achieve population goals (WAZA 2005). Global management practices involve the use of “breeding recommendations”: specific plans indicating which individual animals should be paired to breed. The widely-accepted method for retaining genetic diversity in managed populations is to provide breeding recommendations that pair animals with low and similar mean kinships (average relatedness to the rest of the population) (Lacy 1995; Frankham et al. 2010). Software programs, such as PMx (Lacy et al. 2012), are used to calculate the total population size required to meet the program’s goals and therefore the number of breeding recommendations required each year to produce sufficient offspring, either to offset deaths or for release. Annual breeding targets, however, are always based on a given population’s historical productivity and do not account for changes over generations in captivity. As a result, breeding programs may underestimate the number of breeding recommendations required if productivity has declined, limiting the effectiveness of intensive population management.

Differences between the wild and captive environment may be responsible for changes in productivity. The World Association of Zoos and Aquariums has highlighted adaptation to captivity as a key area for future research, in order to better understand the effects of captive breeding on the long-term viability of captive populations and reintroduction success (WAZA 2005). Genetic adaptation to captivity has been described in fish, insect models, and laboratory mice (Frankham and Loebel 1992; Araki et al. 2007; Lacy et al. 2013), though it is yet to be examined in captive populations of wild mammals (i.e., zoos and other similar intensive management settings). Genetic adaptation to captivity has been experimentally determined as the cause of reduced reproduction in reintroduced steelhead trout after controlling for environmental factors such as rearing environment (Araki et al. 2007; Christie et al. 2012). Species characterized by short generation lengths have a higher risk of adaptation to captivity over time than species with long generation lengths (Frankham 2008). Adaptation to captivity is likely to be a serious problem facing captive species, and “deserves a much higher priority than it is currently receiving” (Frankham 2008, p. 325).

Zoos keep detailed, long-term datasets that are available for analysis (Pelletier et al. 2009; Conde et al. 2011). Our study is the first to statistically model the effect of multiple generations in captivity in a multiple regression framework that controls for other parameters, such as age and institutional experience, that may affect productivity. We examined data from an Australian endemic marsupial, Tasmanian devil (*Sarcophilus harrisi*). The Tasmanian devil insurance population was established in 2006 in response to the catastrophic decline of the wild population due to devil facial tumor disease (Grueber, Peel et al. 2015; Hogg et al. 2015). This insurance population is ideal for answering broad questions about genetic impacts of captive breeding in conservation for two main reasons. First, it is one of the largest conservation breeding programs in the region, so a large dataset is available for analysis. The studbook currently contains over 1685 animals, and pedigree depth ranges from 0–5.625 generations, with 296 animals ≥3rd generation (including breeding data collected from captive devils prior to the establishment of the formal insurance population [Srb 2015]). Note that generation number is defined as 0 for founder animals or as the average generation of the parents plus one for captive offspring (e.g., the offspring of a founder and a first-generation captive-born animal would be considered generation 1.5). Second, the devil insurance population as a whole is distributed over a variety of holding types: from semi-natural island sites with basic monitoring only, to large managed enclosures, and intensive zoo facilities, with a range of human intervention from little-to-no contact to full veterinary treatment (DPIPWE 2010; Hogg et al. 2016). Data from all 20 sites holding the devil insurance population were available for this analysis. The devil program therefore represents the diversity of conservation practices in place today, and acts as an exemplar for the impacts of intensive management on population productivity in conservation. In addition, the devil has a short generation length of 4 years (Woinarski et al. 2014), making it particularly vulnerable to adaptation to captivity. Captive adaptations that affect fecundity could severely limit the ability of released animals to contribute to wild populations (Frankham 2008). Like many other captive breeding programs around the world, the ultimate goal of the devil recovery program is to release devils to ensure an ecologically functional population in the wild (STDP 2014).

In this study, we evaluated seven biological, genetic, and environmental factors thought to influence reproductive success of captive devils using nine years of pedigree-based studbook data and breeding records. Our results have broad implications for the management of threatened species worldwide, and illustrate the value of long-term conservation datasets for the analysis of genetic processes associated with captive breeding.

### Methods

The devil is the world’s largest marsupial carnivore (up to 12 kg) (Owen and Pemberton 2011), and is listed as endangered by the IUCN and under the Australian Environmental Protection and Biodiversity Conservation Act 1999 (EPBC Act) (Woinarski et al. 2014). The Tasmanian devil insurance population is managed by the Zoo and Aquarium Association Australasia (ZAA), the peak industry body in Australasia responsible for the management of 121 captive programs across 90 institutions (Hogg 2013). The Tasmanian devil program is one of the conservation programs managed by the ZAA (Hogg 2013), where monthly data is inputted into the studbook using SPARKS and ZIMS software (Species360 2017). The ZAA uses pedigree data to generate annual breeding recommendations for devils using the mean kinship strategy (Hogg 2013). The full insurance population studbook (from 2006 to 2014) and associated breeding recommendations comprise the starting point for our analysis.

The Tasmanian devil is polyovular and monoestrus, with spontaneous ovulation. Sexual maturity is reached at 1 year, though most females breed at 2 years. Devils have a life expectancy of up to 6 years in the wild (disease-free areas) and 8 years in captivity (Woinarski et al. 2014); and live to approximately 4 years in diseased...
areas (Jones et al. 2008). Devils are seasonal breeders, with females capable of producing one litter each year. Mating occurs in March with births in April after a short gestation period of 31 days, and weaning 250 days after birth (Woinarski et al. 2014). Females can give birth to over 20 early development stage young (Guiler 1970). However, females have only four teats with which to nurse attached immature offspring, so the devil is biologically limited to producing 4 offspring with litter sizes ranging from 1 to 4 (Guiler 1970). The small size of early offspring and female denning behavior (Owen and Pemberton 2011) present challenges for captive managers in accurately determining litter size, and as such offspring accessioned in the studybook (Srb 2015) are commonly those identified at weaning.

Not all breeding recommendations made by ZAA are necessarily attempted by holding institutions, for a variety of logistical and operational reasons. Therefore, our dataset only included animals that were housed together during the breeding season (i.e., breeding was attempted). Our dataset included all 20 insurance population breeding facilities for which data were available, classified into two broad categories: intensive (15) and free-range (5) (Hogg et al. 2015). At intensive sites, breeding recommendations are given to a particular male–female pair, which are housed together when the female comes into estrus; here, the pair is the statistical unit for analysis. At free-range sites, breeding recommendations are given for a group of devils that are housed together and can breed freely. Female reproductive status (number of pouch young) is determined by direct observations at both intensive and free-range sites, but at free-range sites the sire of weaned young cannot always be determined (Hogg et al. 2013); we could not use pairs as the statistical unit for data from the free-range sites. Therefore, we performed 2 analyses: one for “intensive pairs” (based on breeding pairs at intensive sites only) and one for “all females” (encompassing both intensive and free-range females).

Factors thought to influence reproductive success in the devil insurance population were modelled using two response variables: whether an attempted breeding recommendation was achieved or not (i.e., produced at least one offspring; referred to herein as “breeding success”) and number of offspring produced from successful breeding events (referred to herein as “litter size”). Both responses were analyzed for both the intensive pairs and all-females datasets, giving a total of four main analyses. Data were collected for a total of 11 predictor variables across the four analyses, where applicable (Table 1). Sire age, dam age, sire origin (captive-born or wild-born), and dam origin were obtained from the studybook (Srb 2015). PMx (version 1.2.20140905) (Lacy et al. 2012) was used to determine sire and dam inbreeding coefficients, and sire and dam generation. Annual ZAA census data from 2006–2014 were used to obtain number of years since each site first held the species in any given year, and number of holdings of devils at each site each year. “Management type” was also included in our “all females” analyses as a categorical predictor, referring to intensive or free-range sites. In 2007–2008 (the early stages of the program [Hogg et al. 2015]), many pairs were given multiple chances to breed over consecutive breeding seasons, but in more recent years very few devils were given multiple opportunities; we therefore only included the first breeding attempt of a given pair or female (in their lifetime). Data from the first year of the program, 2006, was excluded as most devils were quarantined with only limited breeding (Hogg et al. 2015). Inbreeding parameters could not be included in the analyses as each parameter had a median of 0 with a limited range (only 3/130 females and 4/105 males at intensive sites, and 3/233 females in the all-females analysis had a non-zero inbreeding coefficient, Table 1). The use of pedigree-based management strategies to avoid breeding closely related individuals accounts for the low level of inbreeding in the population.

We evaluated the relationships between our predictor and response variables using generalized linear mixed models, with site and year included in all models as random factors to account for mean differences in reproductive success between institutions and years. The use of a ‘site–year’ explanatory term in our analyses allows us to assess how average breeding success and litter size vary between institutions and years, while the other covariates are examined in relation to those years. Data from the intensive pairs and all-females analyses were included in the same model.

Table 1. Summary statistics for the 2 random effects, 11 fixed predictors of interest and 2 response variables of the 2 datasets [range (mean/ median)]

<table>
<thead>
<tr>
<th></th>
<th>Intensive pairs</th>
<th>All females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of breeding records</td>
<td>239</td>
<td>500</td>
</tr>
<tr>
<td>Unique pairs</td>
<td>182</td>
<td>233</td>
</tr>
<tr>
<td>Sites</td>
<td>14</td>
<td>17</td>
</tr>
<tr>
<td>Sire age</td>
<td>2–6 (3.39/3.00)</td>
<td>1–4 (2.32/2.00)</td>
</tr>
<tr>
<td>Dam age</td>
<td>1–5 (2.85/3.00)</td>
<td>1–4 (2.32/2.00)</td>
</tr>
<tr>
<td>Sire generation</td>
<td>0.00–4.50 (0.78/1.00)</td>
<td>0.00–5.20 (1.04/1.00)</td>
</tr>
<tr>
<td>Dam generation</td>
<td>0.00–5.20 (0.90/1.00)</td>
<td>0.00–5.20 (1.04/1.00)</td>
</tr>
<tr>
<td>Sire origin (captive; wild)</td>
<td>92; 90*</td>
<td>155; 78*</td>
</tr>
<tr>
<td>Dam origin (captive; wild)</td>
<td>110; 72</td>
<td>155; 78*</td>
</tr>
<tr>
<td>Sire F</td>
<td>0.00–0.25 (&lt;0.01/0.00)</td>
<td>0.00–0.25 (&lt;0.01/0.00)</td>
</tr>
<tr>
<td>Dam F</td>
<td>0.00–0.25 (&lt;0.01/0.00)</td>
<td>0.00–0.25 (&lt;0.01/0.00)</td>
</tr>
<tr>
<td>No. years since site held species</td>
<td>0–8 (3.10/3.00)</td>
<td>0–8 (3.10/3.00)</td>
</tr>
<tr>
<td>No. holdings per site per year</td>
<td>2–140 (36.21/23)</td>
<td>2–140 (36.21/23)</td>
</tr>
<tr>
<td>Management (intensive; free-range)</td>
<td>149; 84*</td>
<td>149; 84*</td>
</tr>
<tr>
<td>Breeding success; failure</td>
<td>81; 101 (44.5%; 55.5%)</td>
<td>105; 128 (45.1%; 54.9%)</td>
</tr>
<tr>
<td>Litter size</td>
<td>1–4 (2.72/3)</td>
<td>1–4 (2.71/3)</td>
</tr>
</tbody>
</table>

Entries left blank indicate data were not available, not collected or not applicable.

*Only the first record per female was used; sample size includes N = 149 females from intensive dataset, and N = 84 females from free-range enclosures.

Indicates parameters that were included as fixed effects in the respective global model.
years. Correlations between variables of interest were calculated in R (R Core Team 2013) to determine variable independence and suitability for generalized linear modelling. All correlation coefficients between parameters were below 0.42, so no parameters were discarded at this stage. Global models were generated with the “glmer” function of the lme4 package (Bates et al. 2015) with a binomial logit link. The breeding success/failure response was coded as a binary 1/0. Litter size was modelled as a binomial response (proportion of the maximum litter size of 4) using a 2-column matrix where successes = number of offspring produced and failures = 4 – successes. Because devils are biologically limited to carrying 4 offspring in the pouch (Guiler 1970), this modelling approach prevented our model from predicting biologically impossible litter sizes greater than 4.

To improve comparison of effect sizes within and between models, regression inputs were standardized by subtracting the mean and dividing by 2 standard deviations using the “standardize” function in the arm package (Barton 2015). Model selection and inference were conducted under information theory (Burnham and Anderson 2003). The “dredge” function in the MuMIn package (Barton 2015) was used to obtain all submodels of each global model. Top models were identified as those within 2 AICc (Akaike’s information criterion corrected for small sample size) of the best model (Burnham and Anderson 2003). Model averaging using the natural average method was performed with “model.avg” in the MuMIn package (following Grueber et al. 2011). We evaluated 95% CIs for our final parameter estimates as the point estimate ± 1.96 x the unconditional SE. Inference was based on the relative magnitude of effect sizes and their SEs, 95% CIs, and relative importance (RI) values for each parameter. RI values indicate the probability that a parameter is included in the best model, using the sum of Akaike weights from models containing that parameter (Burnham and Anderson 2003). Examining CIs gives the magnitude, direction, and precision of the parameter (Gelman and Hill 2007). Where parameters demonstrated strong effects (see Results), these were further investigated on the natural scale by back-transforming fitted values using “invlogit” in arm. Parametric bootstrapping with 1000 iterations was used to estimate 95% CIs for back-transformed fitted values.

Results

For the intensive pairs analyses, of the 300 records in the dataset, 61 pairs were excluded due to missing sire information; however, these data were included in the all-females analysis (below). Age, origin, generation, and the two husbandry parameters were included in global models for both responses. One site was excluded from analysis as the dataset included only successful breeding events. The final intensive pairs dataset included the first breeding attempt of 182 unique pairs (comprising 130 females, 105 males). Dam age, dam generation, and number of years since the site held insurance population devils all had strong effects on breeding success with RIs of 1 (Table 2). As dam generation increased, the probability of breeding success declined steadily from an estimated 56.5% in the wild-born generation to 2.8% at generation 5 (Figure 1a). Our results also

Table 2. Summary results of the final models after model averaging: effects of each predictor on breeding success and on litter size in each analysis

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Intensive pairs Breeding success (N = 182)</th>
<th></th>
<th>Intensive pairs Litter size (N = 81)</th>
<th></th>
<th>All females Breeding success (N = 233)</th>
<th></th>
<th>All females Litter size (N = 105)</th>
<th></th>
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<tr>
<td></td>
<td>Estimate (SE) c</td>
<td>RI d</td>
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<td>Estimate (SE)</td>
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</tr>
<tr>
<td>Intercept</td>
<td>-0.43 (0.33)</td>
<td>-0.86, 0.59</td>
<td>0.76 (0.12)</td>
<td>-0.03, 0.15</td>
<td>-0.49 (0.27)</td>
<td>0.52, 0.10</td>
<td>-0.63, 0.04</td>
<td>0.55, 0.96</td>
</tr>
<tr>
<td>Dam age</td>
<td>-1.08 (0.23)</td>
<td>1</td>
<td>0.52, 1.00</td>
<td>-0.28, 0.50</td>
<td>-0.86, 0.30</td>
<td>0.56, 1.08</td>
<td>-0.63, 0.18</td>
<td>0.55, 0.96</td>
</tr>
<tr>
<td>Sire age</td>
<td>-2.74, -0.99</td>
<td>-1.25, 0.58</td>
<td></td>
<td></td>
<td>-0.28, 0.50</td>
<td>0.23</td>
<td>-0.63, 0.18</td>
<td>0.55, 0.96</td>
</tr>
<tr>
<td>Dam origin (wild)</td>
<td>-1.87 (0.45)</td>
<td>1</td>
<td>0.48 (0.30)</td>
<td>-0.11, 0.08</td>
<td>-0.86, 0.30</td>
<td>0.56</td>
<td>-0.63, 0.18</td>
<td>0.55, 0.96</td>
</tr>
<tr>
<td>Sire origin (wild)</td>
<td>-1.90, 1.64</td>
<td>0.37</td>
<td>0.13 (0.65)</td>
<td>0.11</td>
<td>0.48 (0.31)</td>
<td>0.04</td>
<td>0.55, 0.96</td>
<td>0.55, 0.96</td>
</tr>
<tr>
<td>Dam generation</td>
<td>-1.62, -0.28</td>
<td>-1.25, 0.58</td>
<td>-0.90, 1.64</td>
<td>0.27</td>
<td>-0.97, 0.22</td>
<td>0.27</td>
<td>-0.63, 0.18</td>
<td>0.55, 0.96</td>
</tr>
<tr>
<td>Sire generation</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Years since site held species</td>
<td>1.31 (0.57)</td>
<td>0.86 (0.61)</td>
<td>0.20, 2.42</td>
<td>-0.33, 2.06</td>
<td>-0.50 (0.57)</td>
<td>0.24</td>
<td>-0.57, 0.28</td>
<td>0.21</td>
</tr>
<tr>
<td>Holdings/site/year</td>
<td>0.19 (0.24)</td>
<td>0.40</td>
<td>-0.66, 0.28</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Management (intensive)</td>
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</table>

Entries left blank indicate predictors not tested (see Methods); dashes indicate global model predictors that did not appear in the top model set. Italic values correspond with 95% CI.

*Top models before model averaging are presented in Supporting Information: Table S2, Table S4, Table S6, and Table S8.

*Effect sizes have been standardized on 2 SD following Gelman (2008).

*SE represents the unconditional standard error.

*RI is the relative importance of the parameter in the final model.

*Dam origin (captive) was the reference category.

*Sire origin (captive) was the reference category.

*Management (intensive) was the reference category.
showed that an increase in dam age at first breeding decreased breeding success at intensive sites with only a 5.9% chance of breeding success by age 5 in our model (Figure 1b). Breeding success increased with number of years since the site first held insurance population devils from an estimated 19.8% in the first year of holding devils to 75.2% by the eighth year (Figure 1c). In the intensive pairs analysis, the model of litter size included 81 litters; after model averaging, none of the investigated parameters demonstrated strong effects on litter size (Table 2).

For the all-females analysis, which encompassed females from intensive and free-range sites, global model parameters for both breeding success and litter size were dam age, origin, and generation, and management type (intensive/free-range). Three sites were excluded from analysis, one as above, the second as it held devils mainly for quarantine and a third as it has no control over breeding. The breeding success model included the first breeding attempt of 233 females. None of the parameters we investigated demonstrated strong effects after model averaging, although all effect sizes were in the same direction as those of the intensive pairs analysis (Table 2). The litter size model contained 105 litters. Dam origin was the only strong predictor of litter size, with RI of 1 (Table 2). The fitted mean litter size of wild-born female devils was 3.1 joeys (95% CI: 2.76–3.38), much higher than the fitted mean for captive-born females of 2.7 joeys (95% CI: 2.55–2.90) (note that female devils are biologically limited to a maximum litter size of 4, see Methods).

The global models for all four analyses before model dredging and averaging are presented in the Supplementary Materials (Tables S1, S3, S5, and S7). For the top model sets after model dredging was performed see Supplementary Tables S2, S4, S6, and S8.

Discussion

We have demonstrated the value of long-term captive breeding datasets for revealing biological processes that may impact species conservation. The Tasmanian devil insurance population represents an ideal opportunity to evaluate the processes impacting reproductive success in captivity, due to the large size and varied nature of the program. When we analyzed the devil studbook, we observed a substantial decline in devil breeding success as generations in captivity increased (Figure 1a), as well as declining reproductive success of females as age at first breeding increased (Figure 1b). Our observation of larger litter sizes from wild-born females, relative to captive-born females, is consistent with a previous analysis, conducted on a subset of the data used here (Hogg et al. [2015]; using Anova). Overall, our observations present important implications for the intensive management of devils and other threatened species in captivity.

Husbandry Experience

We were able to investigate effects of breeding animals in different sites by including 2 novel measures of institutional experience. Our analysis showed that husbandry experience does influence the reproductive success of devils, as breeding success increased with number of years since the site first held insurance devils (Figure 1c). This trend can be used to inform program productivity going forward: for example, placing “high value” animals such as founders in experienced sites will improve the probability of successful breeding. On the other hand, the number of holdings of devils at a site did not demonstrate strong effects on breeding success or litter size (Table 2). Conde et al. (2011) and Conway (2011) advise that zoos specialize in breeding a few threatened species rather than diversifying, assuming that specialization increases breeding success—our results provide empirical support to this assumption.

Dam Age and Dam Generation

We found that, amongst intensively managed female devils, those that were not given their first opportunity to breed soon after maturity showed greatly reduced probability of breeding successfully (Figure 1b), with only a less than 6% chance of breeding success.
by age 5 in our model. Dam generation also had a strong effect on breeding success, with only a 2.8% chance of breeding success by the fifth generation of captive breeding. Although dam age and dam generation were important predictors of breeding success in intensively managed devils, in the all-females analysis of breeding success (including all intensive and free-range female devils) these parameters did not demonstrate strong effects (Table 2). In fact, none of the parameters we investigated were of importance in the all-females analysis. It is unclear why such differences were observed between our two datasets, although it is possible that differences in husbandry style may be a contributing factor. Females in free-range enclosures are housed in groups instead of pairs and have some level of mate choice. It is also possible that factors such as body weight, density of animals in the enclosure, and behavior may be more important predictors of breeding success in free-range enclosures than the parameters we investigated. Although our pedigree analysis was unable to include these factors, the direction of the effects for dam generation and age was the same across all models (Table 2), suggesting an overall trend.

Adaptation to Captivity

While differences in productivity between wild and captive animals have been documented in many species, including the European mink (Mustela lutreola) (Kiik et al. 2013), island fox (Urocyon littoralis) (Calkins et al. 2013), black stilt (Himantopus novaezelandiae) (van Heezik et al. 2005), black-and-white ruffed lemur (Varecia variegata) (Schwitzer and Kaumanns 2009) and Asian (Elephas maximus) and African (Loxodonta africana) elephants (Clubb et al. 2009), we are not aware of any other studies that have investigated whether productivity in zoo species continues to decline after the first generation in captivity in a multiple regression framework. First-generation declines in the productivity of captive animals relative to wild-born counterparts have been attributed to a variety of factors, including stress, poor body condition and lack of appropriate social development (Levallois and de Marigny 2015). In devils, it is possible that the continual declines we observed, over multiple generations in captivity, may be attributable to similar processes, or other factors. For example, inbreeding can contribute to declines in breeding success in conservation programs (Boakes et al. 2007), although variation in pedigree-based inbreeding metrics was too low to include these parameters in our analyses of devil. Nevertheless, the low variability in pedigree-based inbreeding (Table 1) suggests that conventional measures of inbreeding are unlikely to explain the patterns we observed. That is not to say inbreeding is unimportant for devils, only that current pedigrees are uninformative for predicting the role of inbreeding. For example, at this time insurance population founders are assumed to be unrelated, although it is known that some founders were trapped at least 2 km apart (Hogg et al. 2015), and devils disperse an average of 20 km (Lachish et al. 2011). If some founders were closely related, reduced breeding success with increasing dam generation could result from inbreeding that is unaccounted for in the current pedigree (Rudnick and Lacy 2008). Therefore, generation may be a better predictor of breeding success than inbreeding where molecular inbreeding coefficients are unavailable in the early stages of the pedigree. Molecular resolution of founder relationships, using high-throughput genotyping, may inform these hypotheses and is ongoing (Hogg et al. 2015; Wright et al. 2015).

A further possible cause of the decline in devil productivity with increasing generation times may be selective processes, both in a management and an evolutionary sense. Minimizing adaptation to captivity is one of the key goals of captive breeding programs, along with retaining genetic diversity, however the former is often overlooked in favor of the latter (Montgomery et al. 2010). Under a mean kinship breeding strategy, widely adopted across the zoo industry, animals with low and similar mean kinships are paired in order to equalize founder contributions and minimize inbreeding (see also Introduction; Frankham et al. 2010). This strategy means that, as a program progresses, breeding is increasingly targeted towards underrepresented lineages in order to equalize founder representation (Frankham et al. 2010). If particular lineages are under-represented early on due to heritable characteristics that contribute to poor breeding success, productivity of the population overall is likely to continue to decline as these lineages are increasingly targeted for breeding. Ultimately, demographic considerations may start to outweigh genetic ones, and recalcitrant breeders provided with fewer breeding opportunities. Such a process could result in adaptation to captivity at the population level, especially during the early stages of program establishment, if poor-breeding lineages become progressively more difficult to breed, fail to contribute, and are ultimately out-competed by good-breeding lineages that become favored by population managers in order to ensure population demographic stability. Although our data do not allow us to directly infer whether genetic adaptation to captivity has occurred in the highly managed devil population, opportunities for selection do exist as a result of competitive breeding in group pens, and characteristics of the species reproductive biology (Grueber, Hogg et al. 2015). Ongoing research by our group is examining the genetic basis of these processes.

Conflicts with Strategies to Minimize Adaptation to Captivity

Reproductive senescence has been reported in the devil at about 5 years of age (Jones et al. 2008) and is confirmed in our analyses (Figure 1b). Long non-reproductive periods have also been seen to reduce fertility and shorten the reproductive life of captive elephants and rhinoceroses (Hermes et al. 2004), suggesting the generality of this pattern, in mammals at least. Extending generation length by delaying reproduction is a key strategy used to minimize adaptation to captivity over time and maintain genetic diversity (Williams and Hoffman 2009; Frankham et al. 2010). While there are good reasons to delay reproduction (slower rate of adaptation to captivity, lower risks upon reintroduction), our findings show that delays pose a risk of severely reduced productivity (Figure 1b), which may threaten the goals of the program if these productivity reductions translate to negative population growth and demographic instability. This crucial trade-off between avoiding adaptation to captivity, and maintaining productivity, should be more readily acknowledged and addressed in captive programs, using quantitative means to make informed management decisions about the age at first reproduction.

Regardless of the underlying cause of declining productivity, we have shown that pedigree analysis of captive breeding populations can improve species management, by enabling more-accurate predictions of annual breeding success based on the characteristics of individuals in the population (e.g., dam generations). Detailed modelling of the factors affecting reproductive success in the captive breeding program can provide valuable information for future management, such as new founding events. For example, as no strong sire effects were observed in any of our analyses, we recommend management to prioritize female founders (paired with
captive males), as this strategy will result in larger litter sizes than the reciprocal (pairing a founder male with a captive female), and will maximize founder contributions. We believe that our results are unlikely to be restricted to devils; further analyses in other species will test this hypothesis.

**Conclusions**

We have detailed the practical applications of our results to conservation in captivity and the wild; our results have already been incorporated into the ZAA breeding recommendations for the devil. Importantly, we have shown that the productivity of intensively managed populations changes over time: historical data are a poor predictor of future success. Our results also reveal biological impediments to conservation goals, such as the widely recommended strategy to extend generation length by delaying breeding, which we found limits productivity in the devil. Analysis of captive studbooks can provide valuable data to improve management, and reveal important trade-offs in genetic and demographic goals by implementing strategies to avoid adaptation to captivity. In the short-term, managers may compensate for these declines by planning to undertake more breeding than life-history based software (that does not take into account productivity changes over generations in captivity) predicts. Further research is required to determine whether generational decline in breeding success is correlated with true inbreeding levels or is a result of other factors resulting from the captive environment, such as genetic adaptation to captivity. It cannot be assumed that adaptation to captivity is not occurring in managed captive populations, and we urge further study of diverse species to determine whether this conservation issue is a general trend.

**Supplementary Material**

Supplementary data are available at *Journal of Heredity* online.

**Funding**

Australian Research Council Linkage Projects grant (LP140100508); the Save the Tasmanian Devil Program; the Zoo and Aquarium Association; San Diego Zoo Global; and the Faculty of Veterinary Science, University of Sydney.

**Acknowledgements**

We gratefully acknowledge the studbook holder for the Tasmanian devil, Carla Srbs, for providing pedigree data for this study, and Claire Ford for providing management program information. We also thank all of the Zoo and Aquarium Association member institutions that hold the animals included in the studbook, and the keepers who look after them. We thank Robert Lacy, Derek Spielman and Roslyn Bathgate for comments on an earlier version of this manuscript, as well as two anonymous reviewers for suggestions that improved the manuscript.

**Conflict of Interest**

The authors have no conflict of interest to declare regarding this manuscript.

**Data Availability**

Data deposited at Dryad: [http://dx.doi.org/10.5061/dryad.58ff4](http://dx.doi.org/10.5061/dryad.58ff4).

**References**


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