Assessing the importance of artificial nest-sites in the population dynamics of endangered Northern Aplomado Falcons *Falco femoralis septentrionalis* in South Texas using stochastic simulation models

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Habitat availability might be the most important determinant of success for a species reintroduction programme, making investigation of the quality and quantity of habitat needed to produce self-sustaining populations a research priority for reintroduction ecologists. We used a stochastic model of population dynamics to predict whether attempts to improve existing breeding territories using artificial nest platforms improved the population growth rate and persistence of a reintroduced population of Northern Aplomado Falcons *Falco femoralis septentrionalis* in South Texas. We further assessed whether the creation of new territories, i.e. conversion of entire areas to suitable habitat and not simply the erection of nest platforms, would lead to a subsequent increase in the nesting population. Our model was able to reproduce several characteristics of the wild population and predicted the number of breeding pairs per year strikingly well ($R^2 = 0.97$). Simulations revealed that the addition of nest platforms improved productivity such that the population would decline to extinction without them but is stable since their installation. Moreover, the model predicted that the increase in productivity due to nest platforms would cause the population to saturate available breeding territories, at which point the population would contain a moderate proportion of non-territorial birds that could occupy territories if new ones become available. Population size would therefore be proportional to the increase in available territories. Our study demonstrates that artificial nest-sites can be an effective tool for the management of reintroduced species.

Keywords: endangered species, habitat, habitat restoration, population model, reproduction.

Species reintroduction is an increasingly common practice (Seddon *et al.* 2007, Bajomi *et al.* 2010, Godefroid *et al.* 2011), yet many reintroduction programmes have failed to establish self-sustaining populations (Fischer & Lindenmayer 2000, Ewen & Armstrong 2007, Sheean *et al.* 2012). The quality and availability of habitat to reintroduced populations is perhaps the most important factor determining the success of a reintroduction effort (Griffith *et al.* 1989, Wolf *et al.* 1996, 1998, IUCN 1998, Ewen & Armstrong 2007). For example, the management of food availability and mammalian predators has been important for the re-establishment of forest birds native to New Zealand (Armstrong *et al.* 2002, 2007, Ewen & Armstrong 2007, Armstrong & Seddon 2008). Assessments of habitat area and quality are therefore considered necessary for the success of individual reintroduction programmes aimed at establishing self-sustaining populations and are an overall research priority for reintroduction biologists (Ewen & Armstrong 2007, Armstrong & Seddon 2008, Sheean *et al.* 2012).

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Along with habitat assessment, models of population dynamics are considered essential for reintroduction programmes (Griffith *et al.* 1989, Wolf *et al.* 1998, Seddon *et al.* 2007, Armstrong & Seddon 2008, Armstrong & Reynolds 2012). Indeed, Seddon *et al.* (2007) stated that population modelling should be incorporated into every evaluation of a reintroduction programme not only to assess population viability but also to identify key vital rates and their relationship to management options. For example, population models revealed that reintroductions and increases in habitat available to Florida Grasshopper Sparrows *Ammodramus savannarum floridanus* would improve population viability (Perkins *et al.* 2008). Conversely, Evans *et al.* (2009) showed that releases of White-tailed Eagles *Haliaeetus albicilla* were no longer needed to maintain a population in Scotland.

The Northern Aplomado Falcon *Falco femoralis septentrionalis* is a non-migratory, bird-eating raptor that ranges from Guatemala north to the USA (Keddy-Hector 2000). The species was virtually extirpated from the USA by the early 1900s primarily as a result of losses of brush-free savannah (Hunt *et al.* 2013, USFWS 2014). The last wild Aplomado Falcon nest in Texas was observed in 1941 (Hector 1987) and now the Northern Aplomado Falcon is the only endangered falcon in the USA (Shull 1986, Keddy-Hector 1990). Two reintroduced subpopulations of Northern Aplomado Falcons currently inhabit the open savanna of coastal Texas, including Matagorda and San Jose islands and the area just north of Brownsville (Hunt *et al.* 2013).

Northern Aplomado Falcons depend on nests built by other raptors or corvids, usually in yuccas or mesquites (Hector 1981, USFWS 2014), but they readily accept artificial nest platforms (Jenny *et al.* 2004, Brown & Collopy 2008, 2012, Hunt *et al.* 2013). Nesting productivity is affected by the availability of certain nest substrates (Jenny *et al.* 2004, Brown & Collopy 2008, 2012, Hunt *et al.* 2013). In the absence of tree-yuccas *Yucca treculeana* or nest platforms, which have high rates of productivity, Northern Aplomado Falcons attempt to nest in mesquites or even on the ground, where nesting productivity is low (Jenny *et al.* 2004, Brown & Collopy 2008, 2012, Hunt *et al.* 2013).

The Peregrine Fund, a non-profit conservation organization, first began releasing Northern Aplomado Falcons in 1985, and the population has appeared to be stable since the bulk of releases ended in 2004 (Jenny *et al.* 2004, Hunt *et al.* 2013). Descriptions of the reintroduction and current population characteristics are presented in detail elsewhere (Jenny *et al.* 2004, Hunt *et al.* 2013, USFWS 2014). Breeding productivity for this population has been enhanced by the installation of nest platforms that exclude potential nest predators and competitors. The effect of these nest platforms on breeding productivity has been substantial, with increased daily nest survival rates (Brown & Collopy 2008, 2012) yielding roughly three times the number of fledglings compared with nests in most natural substrates (Hunt *et al.* 2013). Although the effect of nest platforms on productivity is clear, it is important to assess the effects of augmenting breeding sites at a population level (Catry *et al.* 2009).

The provision of nest platforms to Northern Aplomado Falcons might therefore serve as an example of where management of a single aspect of habitat (nest-sites) substantially can improve the quality of the habitat available to a population. Habitat is defined as the conditions necessary for an organism to occupy, survive, and reproduce within a given area (Hall *et al.* 1997). For birds, nest-sites are required for reproduction and can therefore be strong drivers of occupancy (Newton 1998). Because habitat quality is measured as the per-capita rate of population growth (Johnson 2009), management of nest-sites can increase population growth, and therefore habitat quality, through increases in productivity (e.g. Lohmus & Remm 2005, Catry *et al.* 2009, Altwegg *et al.* 2014). The installation of breeding platforms within Aplomado Falcon territories could therefore greatly increase the quality of the habitat available to the population if increases in reproduction are manifested in increased population levels.

Northern Aplomado Falcons in South Texas also appear to be limited by the number of available territories (Hunt *et al.* 2013). Populations of raptors are often limited by the availability of breeding territories and contain substantial numbers of non-territorial birds (floaters) that would breed if more territories were available (Hunt 1998, Hunt & Law 2000). Floaters have been observed in this population (Brown *et al.* 2006), suggesting that territory availability might be limiting. However, limitation by availability of territories has never been formally tested for this population, especially in the context of the

cessation of captive releases and the improvement of productivity owing to installation of nest platforms. It is therefore important to assess territory limitation for this population because the management implications are different than if the population is limited by depressed vital rates such as fecundity or survival, e.g. creation of territories vs. predator management or fecundity enhancement.

It is important to note that the creation of new territories is not as simple as erecting a nest platform in an otherwise suitable area. Because Aplomado Falcons will nest in the absence of nest platforms (or tree-yuccas, Jenny *et al.* 2004, Brown & Collopy 2008, 2012, Hunt *et al.* 2013), the addition of nest platforms to otherwise suitable areas does not necessarily create a new territory, but it does enhance the quality of one already in existence. Therefore, the creation of new territories for Aplomado Falcons would require the management of all aspects of an area that Aplomado Falcons need to survive and reproduce, in addition to a nest platform or tree-yuccas to ensure that the territories are of suitable quality.

Here, we use an individual-based model of population dynamics to examine the efficacy of improving both the quality and the quantity of breeding territories available to the reintroduced population. We assessed whether the installation of nest platforms results in population growth and, conversely, whether the population would decline if nest platforms were no longer maintained. We also assessed whether the amount of available territories limits the population, and whether the creation of new territories would lead to an increase in the number of breeding pairs. We predict that both the maintenance of nest platforms and the creation of additional territories are needed to increase the population.

METHODS

The AploModel

Although many conservation problems can be addressed using simple, single-sex, deterministic matrices (Beissinger & Westphal 1998), the questions that we addressed in this study and the characteristics of the Northern Aplomado Falcon population in South Texas required us to address issues such as stochasticity, differences between sexes, floater survival and transition probability, and nest-site limitation, which cannot be

incorporated into simple methods. We therefore developed the AploModel to be as simple as possible while still accounting for the processes important to the dynamics of the focal population and our research questions.

We briefly describe the AploModel here following the first sections of the ODD protocol (Grimm *et al.* 2010). For full model description and further detail, we have provided a TRACE document (Schmolke *et al.* 2010, Grimm *et al.* 2014) as Appendix S1. We constructed the model in NetLogo 5.2.0 (Wilensky 1999), a free software platform. The model can be run using NetLogo on all major operating systems. All default values are presented in Table 1. The purpose of the AploModel was both to gain a greater understanding of the population of Northern Aplomado Falcons in South Texas, and to examine the efficacy of different management options for the population.

Entities, state variables and scales

The virtual landscape was a 100×100 pixel square. Within the landscape there was a release (or 'hack') tower and a user-defined number of available breeding territories. At initialization, the hack tower and territories were randomly placed within the environment. There was no spatial variation in the quality of the breeding territories. Time moved in 1-year increments. Agents in this model consisted of male and female Northern Aplomado Falcons that maintained a record of their age (ticks, or timesteps), pairing status, territorial status and whether the bird was hacked or born in the wild.

Process overview and scheduling

Hacking
The model 'released' Northern Aplomado Falcons from the hack tower in the same numbers as released per year by The Peregrine Fund in South Texas (Fig. 1a). All birds released were juveniles (age = 0) and all releases were of equal sex ratios.

Settlement
Each year the non-territorial falcons must disperse and try to establish territories. We determined which falcons established territories and paired by having the order of individual settlement dependent upon age and sex. The first segment of the

Table 1. Default parameter values for the AploModel, as well as the standard deviations (sd), definitions, and sources of values.

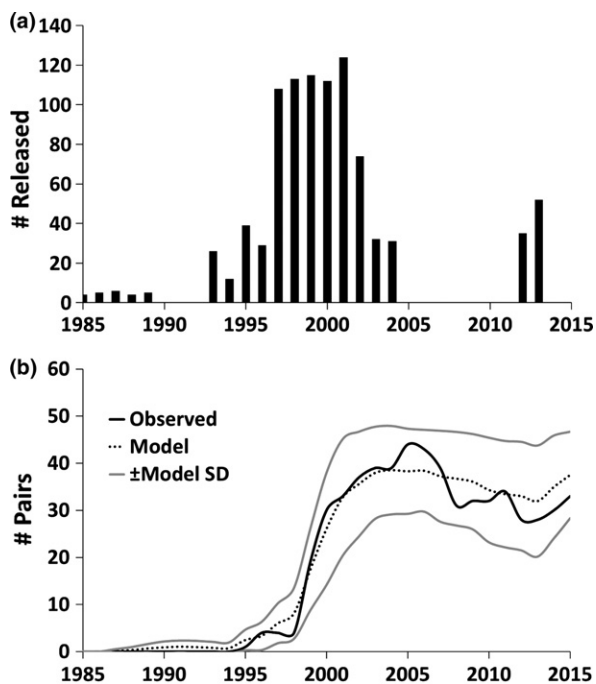| Parameter (variable name)	Definition	Default	sd	Source
Survival – Male Juvenile Wild (MY1Surv)	Probability of wild-born male with age = 0 surviving to next tick	0.18	0.05	Calibration
Survival – Female Juvenile Wild (FY1Surv)	Probability of wild-born female with age = 0 surviving to next tick	0.37	0.05	Brown *et al.* (2006)
Survival – Juvenile Hacked (HackJuvSurv)	Probability of hacked falcon (any sex) with age = 0 surviving to next tick	0.17	0.03	Brown *et al.* (2006)
Survival – Floater Wild (MFloaterSurv, FFloaterSurv)	Probability of wild-born floater (any sex) surviving to next tick	0.87	0.09	Brown *et al.* (2006)
Survival – Floater Hacked (HackFloaterSurv)	Probability of hacked floater (any sex) surviving to next tick	0.30	0.10	Brown *et al.* (2006)
Survival – Breeder (MY2Surv, FY2Surv)	Probability of breeder (any sex) surviving to next tick	0.91	0.08	Brown *et al.* (2006)
Fecundity (pre-2011) (MeanFledge)	Number of fledglings produced per territorial pair	0.86	0.37	The Peregrine Fund, unpublished data
Fecundity (post-2011) (CurrentMeanFledge)	Number of fledglings produced per territorial pair	1.67	0.37	The Peregrine Fund, unpublished data
% Clutch males	Probability a given egg is a male	0.50	NA	The Peregrine Fund, unpublished data
No. Breeding sites (#TerritorySites)	No. of sites available for breeding	44.00	NA	The Peregrine Fund, unpublished data

Figure 1. (a) The number of Aplomado Falcons released by The Peregrine Fund per year in South Texas. (b) The yearly number of breeding pairs predicted by the AploModel under the Status Quo parameterization and observed in the wild. Modelled mean and sd are from 100 simulations.

territories, the falcon became a floater, settling on a pixel without a territory, and did not breed that year. The sub-adult males (age < 2) then settled in the same fashion as the adults, becoming floaters if no territories were available.

After the males had established (or failed to establish) territories, the adult females settled, followed by the sub-adult females. Females paired with males on a territory without taking into account the age of the males. If there were no unpaired territorial males available, females settled in empty territories but did not mate. Only one female could settle on a given territory. If there were no empty territories or unpaired territorial males, the females settled on a pixel without a territory and was a floater. Within each population segment, the order of settlement was drawn randomly. Once a falcon claimed a territory, it remained on that territory until it died.

Productivity

Once pairs formed, those pairs would breed. Each year the average number of offspring fledged was determined by drawing a random number from a gamma distribution with a mean and variance determined using field data (The Peregrine Fund unpubl. data). The model then added to the current year's mean the product of a random yearly value drawn from a distribution with a mean of zero and a standard deviation of one and the observed average

population to settle each year was adult (age ≥ 2) males. These adult males settled on an open territory if available. If there were no available

variance derived from field data. The purpose of this value was to ensure that productivity and survival were positively related (see below). The number of offspring fledged from individual nests was then drawn from a Poisson distribution with the mean being the population mean for that year.

Although nest platforms have been used by this population since the late 1990s, their effect and abundance slowly increased until 2011, when The Peregrine Fund undertook a major effort to improve existing nest platforms as well as erect new ones. The model therefore distinguished between nesting attempts before and after 2011 because of the marked increase in productivity of falcons observed in 2011 (Fig. S1) owing to the installation of improved nesting platforms.

We chose this simple method of modelling changes in productivity as before and after 2011 for several reasons. A model should be as simple as possible to answer a given question (Grimm & Railsback 2005), and implementing an increase in productivity post-2011 was the simplest method of modelling the increase in productivity owing to the implementation of nest platforms. By parameterizing a different mean productivity for the pre- and post-2011 periods the model incorporated the effects of the nest platforms without the complicated process of parameterizing the number and types of different platforms that were either erected or removed/destroyed per year, as well as the reproductive rates within certain iterations of the nest tower design. The ability of the model to recreate several patterns observed in the wild population (Fig. 1b, also see Section 8 of Appendix S1) suggested that this pre- and post-2011 parameterization of productivity was a simple and adequate approximation of productivity for this population over time.

It is certainly possible that some of the difference in productivity between the two time periods was due to a cause separate from the nest platforms, and therefore our modelling exercise might be considered simply a comparison of periods with low vs. high rates of reproduction. However, the sharp increase in productivity after a major installation of nest platforms, which undeniably improved productivity (Jenny *et al.* 2004, Brown & Collopy 2008, 2012, Hunt *et al.* 2013), suggests that the nest platforms were a major driver of the increase in productivity post-2011. Furthermore, our method of parameterizing productivity is likely to lead to a conservative estimate of the effects of the nest platforms. Although productivity was substantially lower during the pre-2011 period, efforts to design and erect nest platforms during that time slightly increased productivity above what it would be in the complete absence of nest platforms. Therefore, comparing productivity between the pre- and post-2011 periods is likely to under-estimate the true effects of nest platforms on productivity, making our results conservative.

The mean of the annual productivity of the breeding population both pre- and post-2011 and the variance can be set by the user. The sex of each offspring was determined by comparing a random uniform value between 0 and 1 to the average sex ratio set by the user. If the random value was below the set sex ratio, the offspring was male, otherwise it was female.

Survival

During each year the population-wide mean of survival was determined by the formula mean + $Z*$sd, where Z was the same Z-score described above for productivity and the mean and sd for each subset of the population were set by the user. The particular fate of each falcon was determined by a random Bernoulli trial with the mean being the mean of that year.

Design concepts

Basic principles

The order of settlement among life-stages was based on field observations and followed the typical raptor pattern of becoming floaters if no breeding sites were available (Hunt 1998). One of the downlisting criteria for this species is that the population be self-sustaining (Keddy-Hector 1990, USFWS 2014). The model therefore assumed no immigration so that we could assess whether the population could sustain itself without immigration from other areas. Of course, immigration should increase population viability (e.g. Stacey & Taper 1992), but the nearest known population occurs hundreds of kilometres to the south in coastal Mexico (USFWS 2014) and there is little known immigration. Population dynamics emerged from interactions between the processes of hacking, productivity and survival, as well as the number of available breeding territories.

Agents interacted by finding mates of the opposite sex and were excluded from territories by members of the same sex.

Stochasticity

Stochasticity was a property of the model at both the yearly and individual levels. Average values of survival and productivity were drawn randomly every year, and individuals drew random values to determine outcomes (e.g. live or die, number and sex ratio of offspring fledged).

Observation

The overall population size and numbers of each sex as well as number of breeding pairs, floater-to-breeder ratio, age ratio of breeding pairs, number of lone males and females, and proportion of breeding pairs with sub-adult males or females were observed during each simulation.

Simulations

We simulated population dynamics for the years 1985–2085 using several parameterizations that simulate different management scenarios to examine the efficacy of both improving the quality of breeding territories (e.g. erecting nest platforms within established territories) and the quantity of habitat by creating more breeding territories. These parameterizations were: (1) a 'Status Quo' parameterization that simulated the processes that created the field data and assumed that those processes will continue, on average, into the future; (2) a 'No Platforms' parameterization that assumed that the quality of habitat was never improved through the installation of nest platforms; and (3) an 'Add Territories' parameterization that assumed that 20 additional territories were created in the year 2020. All parameterizations were the same regarding the hacking and settlement procedures and only varied in their parameterizations of productivity and the number of territories available. There was no spatial heterogeneity in territory quality (i.e. productivity) under any parameterization. These three parameterizations allowed us to compare population dynamics under different management scenarios where the quantity and quality of territories were manipulated. We ran 100 simulations of each parameterization, each of which lasted either until 2085 or until the population declined to extinction, whichever came first.

Status Quo model

The 'Status Quo' was the model parameterization that used values derived from field data, which included nest platforms, and calibration of juvenile male survival (Appendix S1). This parameterization was used as a null model from which we determined the utility of the model and compared it with other parameterizations where parameters were changed to simulate management actions (or inactions). The number of territories available was set to 44, as that was the maximum number of occupied territories observed (USFWS 2014) and is likely to be the number of serviceable territories currently available (P. Juergens pers. obs.). The survival rate and sd for each subset of the population was set to the values estimated by Brown *et al.* (2006) except for the survival of juvenile males, which was calibrated to match a subset of the observed patterns in field data (Appendix S1). The Status Quo also set the average productivity of the population to either observed pre-2011 (0.86 fledglings/attempt) or post-2011 (1.67 fledglings/attempt), depending on the current year of the model (Appendix S1).

No Platforms

The 'No Platforms' parameterization was the same as the 'Status Quo' but assumed that productivity was constant at the pre-2011 rate of 0.86 fledglings/attempt, on average, throughout the entire simulation. In other words, productivity did not increase to 1.67 fledglings/attempt after 2011, because no nest platforms were erected. Therefore, this parameterization, when compared with the Status Quo, tested the efficacy of improving the quality of existing habitat using nest platforms. Note that this parameterization was likely to be optimistic in terms of population levels because efforts to test and erect nest platforms prior to 2011 are likely to have increased productivity slightly over background levels.

Add Territories

The 'Add Territories' parameterization was also a variation of the 'Status Quo'. The only difference was that we add 20 breeding territories in the year 2020, a parameterization that tested whether the creation of territories would lead to an increase in the number of pairs when compared with the Status Quo. It is important to note that productivity within the territories added in 2020 was the same as the already-existing territories. These new territories did not simply represent the addition of nest platforms to otherwise suitable areas, but instead the conversion of unusable areas to habitat of similar quality to the existing territories containing nest platforms.

Sensitivity analysis

We conducted sensitivity analysis on all parameters in this model excluding the variances around those parameters. Thus, we systematically varied the survival rates for juvenile males, juvenile females, adult breeding males, adult breeding females, floater males, floater females, hacked juveniles and hacked floaters, but did not change the amount by which they vary by time-step. In addition, the mean number of fledglings (both before and after quality improvement), the proportion of male fledglings and the number of breeding sites were also varied. For each parameter we conducted 100 simulations in which all other parameters were held constant but the parameter of interest was varied from baseline in increments within a biologically realistic range. This resulted in a total of 12 100 simulation runs. Output for these simulations was the number of breeding pairs, the year of extinction and the floater to breeder ratio. The results of these simulations were then analysed using the 'spartan' package (Alden *et al.* 2013, 2014) in program R (version 3.1.1; R Core Team 2012). For all response variables, a Vargha–Delaney A-Test (with the standard significance level of 0.21) was conducted when varying each parameter.

RESULTS

Matching model output to observed patterns

We evaluated the utility of the AploModel by determining which patterns in field data were also approximated by the Status Quo parameterization. The AploModel matched all eight of the observed patterns against which it was tested (Appendix S1). Perhaps most striking was the ability of the model to replicate the number of pairs observed per year in the wild (Fig. 1b). Both the modelled and the observed number rose until roughly 2005 and then declined following the cessation of captive releases (Fig. 1). Then, in about 2013, the number of pairs increased again, consistent with increases in productivity and additional releases in 2012–2013 (Fig. 1). Indeed, in addition to these qualitative descriptions of the changes in the numbers of pairs over time, the observed and modelled changes in the number of pairs per year were strikingly correlated ($R^2 = 0.97$). It should be noted that the number of pairs per year predicted by the AploModel was not simply driven by the number of falcons released ($R^2 < 0.01$), but instead was an emergent property of the number of falcons released and their ability to survive, reach breeding status, and fledge offspring. Indeed, the number of juvenile birds released would not increase the number of breeding pairs if juveniles could not survive to breeding age. Additionally, the population would not persist after the cessation of releases without appropriate levels of survival and reproduction. The ability of the AploModel to predict the number of pairs observed per year (and other patterns) lent confidence to its ability to predict the effects of management actions on the number of breeding pairs in the population.

Importance of nest platforms

We compared the Status Quo parameterization, which included an observed increase in productivity in 2011 due to the installation of improved nest platforms, with the No Platforms parameterization, which held productivity constant at pre-platform levels. The results of the No Platforms simulations revealed that the population could not sustain itself under the levels of productivity observed before nest platforms were installed (Fig. 2a), in contrast to the Status Quo parameterization, in which the median number of pairs at the end of each model run was 44, suggesting the population was constant and had saturated the available habitat. Indeed, the median year of extinction for the 100 simulations under the No Platforms parameterization was 2056, whereas the median simulation under both the Status Quo and Add Territories parameterizations lasted the full 100 years (2085; Fig. 2a). Furthermore, at the end of the simulation runs, both the Status Quo (median = 0.59) and the Add Territories (median = 0.65) parameterizations had moderate ratios of floaters to breeders, whereas floaters were nearly non-existent under the No Platforms parameterization (median = 0.00; Fig. 2b).

Territory availability

In addition to testing the importance of nest platforms, we also examined the effect of adding habitat using the Add Territories parameterization. When 20 territories were added to the simulations in the year 2020, the simulated populations increased to saturate the available habitat (Fig. 2c)
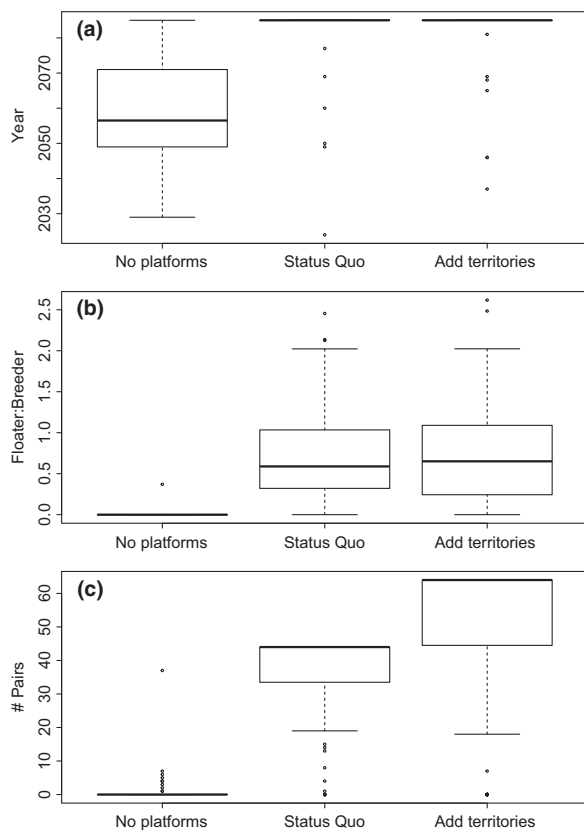
Figure 2. Boxplots representing: (a) the final year at the end of 100 simulations; (b) the ratio of floaters (non-territorial birds of breeding age) to breeders; and (c) the number of breeding pairs under the No Platforms (which assumes that productivity remains at the low level of 0.86 fledglings per attempt for the whole simulation), Status Quo (which assumes that productivity increased to 1.67 fledglings per attempt in 2011), and Add Territories (which is the same as the Status Quo except 20 new potential breeding territories are added in 2020) parameterizations. Each simulation ran for 100 years or until the population declined to extinction.

with a median population size of 64 pairs at the end of each model run. Comparison of the Add Territories and the Status Quo parameterizations revealed that the addition of 20 territories led to an increase of roughly 20 breeding pairs (Fig. 2c), with the median simulation reaching 60 pairs in the year 2037.

Sensitivity

Sensitivity analysis revealed that the number of breeding pairs, the year of extinction and the floater to breeder ratio were most sensitive to changes in breeder survival. Indeed, all measures of model output were significantly affected when estimates

of breeder survival decreased below roughly 80% of the default value (see Section 7 of Appendix S1 for further details).

DISCUSSION

Our results demonstrate the importance of managing artificial nest-sites for the maintenance and growth of the reintroduced population of Northern Aplomado Falcons in South Texas. The ability of the AploModel to match the patterns observed in the field, especially the observed number of breeding pairs per year, suggests that it is useful for examining the effects of management actions on population dynamics. Importantly, under certain management scenarios the simulated populations reached Moffatt's Equilibrium (Moffat 1903, Hunt 1998), whereby all territories were occupied and a contingent of individuals of reproductive age were unable to gain a territory. These non-territorial individuals had to forgo reproduction and become floaters. Populations at Moffat's Equilibrium are therefore limited by the availability of breeding territories (Moffat 1903, Hunt 1998). Although they do not reproduce, floaters are important in buffering the breeding population against loss by replacing dead breeders (Hunt 1998, Penteriani *et al.* 2005a,b, 2006, 2008, 2011). Moreover, a population with floaters is a ready source of recruits, able to colonize new sites (Hunt 1998). When a population reaches Moffat's Equilibrium and has saturated available sites, the observed increase of the population will be zero because there is no room for expansion. Habitat quality for populations at Moffat's Equilibrium should therefore be judged not by the observed rate of population growth but instead by the potential for growth, which can be measured by the number of floaters.

Simulations revealed that the increase in productivity due to the installation and improvement of nest platforms had halted population declines and should cause the population to grow to saturation, eventually reaching Moffat's Equilibrium (Fig. 2b,c). Conversely, if nest platforms were no longer maintained, the population would be likely to decline to extinction. Therefore, because nest platforms changed the population from one that would decline to extinction to one that was growing, we argue that nest platforms greatly enhanced the quality (Johnson 2009) of territories available to Northern Aplomado Falcons in South Texas.

That populations under the Status Quo and Add Territories parameterizations increased, reached Moffat's Equilibrium, and then developed floaters demonstrated the power of manipulating nest-sites to improve the quality of habitat available to a population. Past studies demonstrate that artificial nest structures can bolster raptor populations, especially when those structures increase nest success. For example, providing artificial nest-sites for Lesser Kestrels *Falco naumanni* reduced the predation rate on nests and increased the population growth rate in Portugal (Catry *et al.* 2009). Similarly, nestboxes increased the productivity of a population of Peregrine Falcons *Falco peregrinus* in Cape Town, South Africa, which helped increase population levels (Altwegg *et al.* 2014). The population of Northern Aplomado Falcons in coastal Texas offers further evidence that the provision of artificial breeding sites can be an effective management tool.

The most important effect of provisioning nest platforms is that far more floaters are produced than would be the case if platforms were never erected. Indeed, both the parameterizations (Status Quo and Add Territories) that assumed an increase in productivity after 2011 due to the installation and improvement of nest platforms produced floaters, whereas the No Platforms parameterization produced almost none. The production of floaters indicates that because of the installation of nest platforms, the population can act as a source, with floaters able to colonize new territories if they become available. The Add Territories parameterization tests this demographic potential (*sensu* Lande 1987) of the population by adding 20 territories in the year 2020. The simulated populations fill the newly created territories because floaters are available to colonize the new sites. Once the new territories are filled, the population reaches a new equilibrium, with floaters available to colonize new sites if they became available.

A downlisting criterion for this species is a self-sustained population of at least 60 breeding pairs (USFWS 2014). Our simulations revealed both the obvious fact that there will not be 60 pairs unless there are 60 serviceable territories, and that the population has the demographic potential eventually to fill 60 territories, if made available. As for self-sustainment, the nest platforms compensate for the scarcity of tree-yuccas, which, unlike mesquite and huisache, offer effective

protection from ground predators (Hunt *et al.* 2013). Restoration of natural yucca-savanna may eventually render the nest platforms superfluous.

The AploModel incorporated demographic and environmental stochasticity, both important aspects of population modelling (Morris & Doak 2002). The model does not, however, account for parametric uncertainty or possible catastrophes potentially reducing our absolute estimates of extinction time (Morris & Doak 2002, McGowan *et al.* 2011). That the populations simulated using the Status Quo parameterization rarely reach extinction should not be interpreted as a negligible risk of extinction. Instead, the comparison of the populations simulated under the Status Quo and No Platforms parameterizations, which generally reach extinction around 2056, revealed that provisioning of nest platforms changed the population from one that was declining to one with the potential for expansion and therefore a substantially decreased risk of extinction. The AploModel, therefore, should be useful in weighing management options for this population of Northern Aplomado Falcons.

Sensitivity analysis revealed the vital rates that most affected model outputs, and therefore where parametric uncertainty would most likely sway inference. The number of pairs at the end of a simulation under the Status Quo parameterization was the most sensitive to changes in adult survival (see Section 7 of Appendix S1), a phenomenon characteristic of populations of long-lived birds (Sæther & Bakke 2000, Clark & Martin 2007). Therefore, changes in or mis-estimation of adult survival would bias inference based on our parameterizations. Furthermore, adult survival is a useful measure of the current health of a population of long-lived raptors (Katzner *et al.* 2007). Therefore, ringing and resighting should be a monitoring priority for this population so that the precision of survival estimates can be improved, and the cause of any changes in survival can be identified and addressed.

Additional ringing and resighting would also elucidate apparent differences between the survival of males and females. Although Brown *et al.* (2006) did not find different rates of survival between sexes, more lone females than males and more pairs with sub-adult males than pairs with sub-adult females have been observed throughout the history of this population (Hunt *et al.* 2013). We therefore calibrated the survival of juvenile

males to a level that produced a number of lone territorial females close to that observed in the wild (Appendix S1). Note that we only used one pattern and one parameter for calibration and therefore the ability of the AploModel to match other patterns should not be attributed to overfitting of parameters. Furthermore, inference from our results was insensitive to the parameter calibrated, i.e. regardless of the parameter calibrated, populations declined under the No Platforms parameterization and reached equilibrium under the Status Quo and Add Territories parameterizations (Appendix S1). Our results suggested the hypothesis that differences in juvenile survival between sexes drive observed differences in sex ratios. However, further research should empirically test this hypothesis and search for a biological driver of differing rates of apparent survival between sexes.

Although the AploModel revealed that habitat creation and management can positively affect the population of Aplomado Falcons in South Texas, it did not address the ideal spatial arrangement and characteristics of created habitat or the cost of such efforts. Creating new territories would probably require the creation of more brush-free savannah which includes either nest platforms or tree-yuccas (Hunt *et al.* 2013). Future studies should examine the habitat characteristics that influence occupancy and demography of this population (USFWS 2014) as well as examine the propensity of dispersing individuals to colonize new areas. Tracking devices might also aid in studying habitat use and dispersal. Our modelling also suggested that as long as reproduction remains high, and survival remains at observed levels, the population might be stable. The USFWS (2014) suggested that downlisting criteria for the Northern Aplomado Falcon might be reassessed with new information regarding habitat suitability. The AploModel might therefore be useful in evaluating the downlisting criteria for this species.

Our results not only provide management and monitoring recommendations for Northern Aplomado Falcons in South Texas but also support assertions by other authors that assessments of both the quality and the availability of habitat are imperative for reintroduction programmes (Griffith *et al.* 1989, Wolf *et al.* 1996, 1998, IUCN 1998, Ewen & Armstrong 2007). This study underscores the utility of population modelling not only for understanding the dynamics of reintroduced populations, but also for examining the efficacy of management options and identifying the most influential vital rates (Griffith *et al.* 1989, Wolf *et al.* 1998, Seddon *et al.* 2007, Armstrong & Seddon 2008, Armstrong & Reynolds 2012).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. TRACE document.