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Wild-reared aplomado falcons survive and recruit at higher rates than hatched falcons in a common environment

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ABSTRACT

The northern aplomado falcon (*Falco femoralis septentrionalis*) has been the subject of a large-scale reintroduction effort conducted by The Peregrine Fund since 1993. Intensive monitoring during 2002–2004 revealed approximately 38 breeding pairs and numerous non-territorial individuals in two study areas centered on Matagorda Island National Wildlife Refuge (NWR) and Laguna Atascosa NWR. Continued releases (“hacking”) of captive-bred young after pair establishment and successful wild breeding provided an opportunity to compare survival and recruitment histories of wild-reared and hatched falcons hatched during 2001–2003. We used Program MARK to rank multi-state models of apparent survival and recruitment rates with Akaike’s Information Criterion scores, corrected for small samples. The top model candidate, with almost 3.5 times more support than the next best model, detected differences due to falcon origin (wild or captivity): although breeder survival was independent of origin, juvenile hatched falcons survived and recruited at lower rates than wild-reared falcons. Given the high density of territorial adult falcons in the study areas, the difference in apparent survival may reflect greater dispersal by hatched falcons, increased tolerance of wild falcons in territory margins due to prior socialization, or other factors effecting higher intrinsic fitness of wild falcons. However, natal dispersal did not differ between the two groups, strengthening the hypothesis of a difference in true survival. Disproportionately greater recruitment of wild falcons into the breeding population again suggests their higher intrinsic fitness. These findings show how close monitoring of population vital rates can efficiently guide adaptive management of recovering populations.

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1. Introduction

Recent approaches to conservation of endangered or threatened species have turned proactive, with advances in captive breeding and translocation techniques leading to increasing numbers of reintroduction, translocation, and supplementa-

tion projects (Cade and Temple, 1995; Sarrazin and Barbault, 1996). Reintroduction projects may generate large amounts of field data, particularly when animals are marked before release and monitored afterwards, often for years or even decades (Sarrazin and Barbault, 1996; Fischer and Lindenmayer, 2000). In addition to applications to adaptive management,

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such data may be relevant to analyses of colonization and dispersal patterns, founder effects, short-term adaptation to novel environments, or species life history traits (Sarrazin and Barbault, 1996, but see Armstrong and Ewen, 2001; Kauffman et al., 2004; Schaub et al., 2004).

Previous studies of reintroduced populations have posited that reintroduced and/or translocated animals have lower survival rates than wild-produced conspecifics (Griffith et al., 1989; Fischer and Lindenmayer, 2000; but see also Nicoll et al., 2004). Pitfalls in interpretation may, of course, arise when apparent survival rate is indistinguishable from return rate or is confounded by location effects or by interannual variation in climate or food availability. Even so, advances in analyses of mark-recapture data now allow rigorous investigations into a wide array of biological hypotheses (Cooch and White, 2004). Multistate (or multistrata) models can simultaneously estimate apparent survival rates and recapture probabilities for individuals in multiple locations and/or observable physical states, as well as the probabilities that individuals will transition between the different states (Brownie et al., 1993). When breeding status (non-breeder or breeder) is considered as a state, the transition probability corresponds to recruitment into the breeding population (Pradel and Lebreton, 1999).

For our purposes, application of a multistate model to mark-recapture data derived from a reintroduced population allows the use of both survival and recruitment rate as a means to evaluate the relative fitness of groups within the population. We here analyze resighting data of northern aplomado falcons (*Falco femoralis septentrionalis*) in southern Texas where a long-term reintroduction project was conducted by The Peregrine Fund beginning in 1993 (Jenny et al., 2004). Captive-bred falcons, released by a “soft release” procedure, known as “hacking,” rapidly established a wild-living breeding population. Continued releases of captive-bred (hereafter, “hacked”) falcons in the presence of breeding adults and their offspring through 2004 provided the opportunity to simultaneously compare demographic rates of hacked and wild-reared (hereafter, “wild”) falcons in a common environment. The comparison was based on two distinct measures of the relative fitness of falcons of differing origin: survival and recruitment.

2. Methods

2.1. Study organism and site

The northern aplomado falcon, whose range centers in Latin America, was extirpated from the United States by the 1950s (Keddy-Hector, 2000). This medium-sized (females, 406.7 g, $n = 6$; males, 260.5 g, $n = 8$), savanna-dwelling falcon specializes in hunting avian prey, often cooperatively (Hector, 1981; Brown et al., 2003). Breeding pairs are highly territorial and reside on territories year-round (Jenny et al., 2004). Releases were concentrated in two areas: the Rio Grande Valley in the vicinity of Laguna Atascosa National Wildlife Refuge in Cameron County (26°5'N, 97°21'W) and the Texas Coastal Bend encompassing Matagorda Island NWR and Aransas NWR (28°14'N, 96°37'W). Occupied habitat is open coastal plain with widely interspersed small shrubs and trees.

2.2. Hacking procedure

Jenny et al. (2004) provide details of The Peregrine Fund's captive-breeding program and hacking procedures. Before release, all falcons (over 800 individuals in all) were banded with USFWS bands and, since 1998, colored aluminum visual identification (VID) bands with unique alphanumeric characters on the opposite tarsus. Batches of 2–8 fledging-age falcons were released together from elevated platforms; attendants provided food until independence. We monitored falcons at the release site, and those resighted 21 days or later post-release were considered to have reached independence.

2.3. Wild population monitoring

Nest-searching was opportunistic during 1995–2001 and, although 53 chicks were banded in wild nests, most breeding adults remained unidentified. Beginning in 2002, we systematically searched for pairs before the onset of breeding activity, identified individuals by visual inspection of their bands, and followed nesting attempts from initiation through post-fledging. The natural tameness and approachability of aplomado falcons, whether hacked or wild, enabled us to identify all banded, breeding adults by means of standard spotting scopes (Keddy-Hector, 2000). Survey effort was equal across years, with three full-time field biologists searching for falcons annually. Unlike colonial seabirds and other avian taxa in which recruitment rates have been investigated (Nichols et al., 1994; Reed et al., 2003), non-breeding aplomado falcons were observable, and some were later found paired. Falcons that attempted nesting (laid and incubated eggs) were recorded as “breeding,” whereas all others, whether territorial or apparently transient, were considered “non-breeding.” Wild chicks in accessible nests were banded when approximately 21-d old with USFWS and VID bands. We later visited nests to confirm fledging, as verified by observing fledglings in flight or sighting them in locations accessible only by flight.

2.4. Mark-recapture analysis

Encounter histories were constructed from the combined banding records of hacked and wild falcons and subsequent resighting records. We restricted our analyses to those falcons hatched during 2001–2003, since numbers of hacked and wild falcons fledged were comparable in those years. Resighting records from 2002–2004 also were considered, as the breeding population was then closely monitored, allowing us to detect recruitment. Only those hacked falcons deemed independent and wild falcons confirmed as fledged were included in the analysis, in order to exclude early hack-site or nest-site mortality. Multiple sightings in a season were treated as a single record. We used these encounter histories as an input file for program MARK (White and Burnham, 1999), and we divided the population into groups based on sex and origin (hacked or wild). We used the multistate model structure to model apparent survival rates (ϕ), resighting rates (p), and probability of transition from non-breeding to breeding state (ψ_{nb}) (Pradel and Lebreton, 1999). Unlike previous published multistate studies of recruitment rate, our non-breeding individuals were observable, so the resighting rate for this state

(p_n) did not have to be fixed to 0 (Pradel and Lebreton, 1999). We assumed that recruitment into the breeding population was permanent ($\Psi_{bn} = 0$).

Since raptor age-classes are widely recognized to survive at differing rates, our most general model included juvenile and adult age-classes for the non-breeding state and full time dependence for the remaining parameters (Brown and Amadon, 1968; Newton, 1986). Accordingly, we tested model goodness-of-fit for our general model by using the median c-hat procedure implemented in program MARK, which is appropriate when the most general model is not fully time-dependent (Cooch and White, 2004); the median c-hat procedure calculates a variance inflation factor (c-hat). Models were selected using quasi-likelihood-adjusted Akaike’s information criterion adjusted for small sample size (QAIC_c; Burnham and Anderson, 2002). We constructed reduced-parameter models by sequentially finding the best-fitting model of resighting probability, then apparent survival, then recruitment rate. Because top models consistently failed to converge on an estimate for adult survival rate, presumably due to the parameter’s proximity to 1.0, we utilized the Bayesian parameter estimation procedure (MCMC or Markov Chain Monte Carlo) available in program MARK to obtain parameter estimates. Preliminary MLE parameter estimates (logit link function) served as the priors for the MCMC estimation (Cooch and White, 2004).

3. Results

3.1. Resightings

During 2001–2003, 141 captive-bred falcons reached independence in southern Texas. Concurrently, 75 banded chicks fledged from nests in the study area. During 2002–2004, we resighted 43 of these falcons (19 hacked and 24 wild) at least once. Eighteen (three hacked and 15 wild) were recruited into the breeding population; nine were from the 2001 cohort, eight from 2002, and one from 2003.

3.2. Model selection

Our most general model fit the data adequately, with the median c-hat value (1.1643) indicating only a minor degree of overdispersion. Subsequent model selection was based on QAIC_c scores generated by incorporating this variance inflation factor. Resighting rate (p) was modeled first, and as res-

ighting effort was uniform throughout the study’s duration, the selection of a constant resighting rate as the most parsimonious was logically plausible. Our most general model considered non-breeder survival (ϕ_n) incorporating two age-classes interacting with origin and sex, whereas breeder survival was better modeled without a sex effect (Table 1). Inclusion of sex, origin, time, or their interactions did not improve the performance of the models, so survival of breeding falcons (ϕ_b) was best described as constant (Table 1). In the overall best model, falcon origin was the only term affecting recruitment rate (Ψ_{nb} ; Table 1).

In summary, the most parsimonious model detected effects on non-breeder survival correlated with origin (hacked or wild) and age class, an effect also present in the six next-best-fitting models, with a combined model weight of 0.9996 (Table 1). Recruitment rate also was correlated with origin in the top model, as well as in two out of the following three models, combining for a model weight of 0.7835. Resighting probability and breeder survival were modeled as constant in the top five models.

3.3. Parameter estimates

Because the difference in QAIC_c scores between the best-fit model and the next most competitive model was greater than 2, indicating generous support for the first model alone, we derived parameter estimates solely from the first model (Table 2; Burnham and Anderson, 2002). Among non-breeding falcons, both age-classes of hacked falcons had lower apparent survival rates than their wild counterparts (Fig. 1). Juvenile falcons, regardless of origin, survived at lower rates than adult non-breeders and breeders, but adult non-breeding wild falcons survived at rates similar to breeding falcons (Fig. 1). Wild falcons had a higher annual probability of recruiting into the breeding population than hacked falcons (Table 2).

4. Discussion

4.1. Limitations of the multistate model

The multistate model structure explicitly models apparent survival rates, as the structure assumes that movement is restricted to the described states such that permanent emigration does not occur (Reed et al., 2003). Whereas this assumption is unrealistic, our conclusions would be affected

Table 1 – Top six models fitted to the encounter histories of captive-bred and wild-reared aplomado falcons

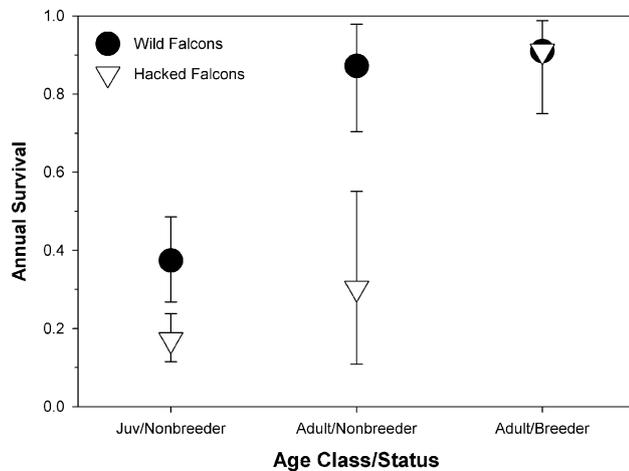
Model	Non-breeder survival (ϕ_n)	Breeder survival (ϕ_b)	Resighting (p)	Recruitment rate (Ψ_{nb})	QAIC _c	Δ QAIC _c	QAIC _c weight	No. parameters	Deviance
1	Origin, two age-classes	Constant	Constant	Origin	313.30	0.00	0.55	9	72.00
2	Origin, two age-classes	Constant	Constant	Origin, sex	315.78	2.48	0.16	11	70.13
3	Origin, two age-classes	Constant	Constant	Constant	316.02	2.72	0.14	8	76.87
4	Origin, sex, two age-classes	Constant	Constant	Origin, sex	317.38	4.08	0.07	15	62.80
5	Origin, two age-classes	Constant	Constant	Annual	318.04	4.74	0.05	10	74.57
6	Origin, sex, two age-classes	Origin	Constant	Origin, sex	319.66	6.36	0.02	16	62.80

Models are listed in order of Akaike’s information criterion values corrected for variance inflation (QAIC_c).

Table 2 – Parameter estimates from top model of survival and recruitment rates for aplomado falcons

	Apparent annual survival rate						Recruitment rate	
	Juvenile non-breeder (ϕ_j)		Adult non-breeder (ϕ_n)		Adult breeder (ϕ_b)		(ψ_{nb})	
	Estimate	LCI-UCI	Estimate	LCI-UCI	Estimate	LCI-UCI	Estimate	LCI-UCI
Wild falcons	0.374	0.268–0.486	0.872	0.704–0.979	0.910	0.750–0.988	0.387	0.266–0.517
Hacked falcons	0.171	0.115–0.238	0.303	0.109–0.551	0.910	0.750–0.988	0.147	0.054–0.264

“LCI” and “UCI” are lower and upper 95% confidence intervals.

**Fig. 1 – Estimates of aplomado falcon annual survival rates from top model (error bars are 95% CI; “Juv” are falcons in the juvenile age class).**

mainly by a difference in emigration rates between groups. If such a difference exists, this could indicate that hacked falcons have either an increased intrinsic propensity to emigrate, or decreased ability to reside in close proximity to territorial adults. Differences in natal philopatry have been reported between hacked and wild raptors, as well as between sexes (Evans et al., 1999; Amar et al., 2000; Lieske et al., 2000; but see also Tordoff and Redig, 1997). Whereas our scope of inference is limited by sample size and study duration, the falcons comprising our study population did not differ in dis-

tance dispersed from natal site to nesting attempt location (median km dispersed by wild falcons = 31.72, by hacked falcons = 33.34; Wilcoxon rank sum test, $W = 18$, $p = 0.6544$). With that consideration, we hypothesize lower survivorship among the hacked cohorts.

Reduced survival rates among hacked falcons during our study could be derived from the lack of parental influence potentially reducing foraging ability, resistance to the elements, especially predation, or the ability to socialize with adults. Such traits are difficult to evaluate under field conditions, and investigation into mechanisms underlying survival differences would require behavioral experiments under controlled settings (Mathews et al., 2005). In any case, regardless of whether apparent survival differences derived from differences in natal philopatry or higher true survival rates, wild falcons became disproportionately represented in the local population in the years following fledging.

4.2. Survival and recruitment estimates

As noteworthy as the difference in apparent survival between juvenile hacked and wild falcons is the uniformly high apparent survival rate of adult breeding falcons regardless of origin. The disappearance of survival rate differences in recruited individuals suggests a fitness threshold beyond which falcons, whether hacked or wild, are equally competitive in the south Texas environment. Higher survivorship of the breeding population can be attributed both to the intrinsic high fitness of recruited falcons as well as advantages garnered by residence in a fixed territory, including knowledge

Table 3 – Survival rates, estimated using recent software, reported for other raptor species for comparison; falcon species (genus *Falco*) are closely related to aplomado falcons

Species	Survival rates			Source
	1 year	2 year	Adult	
<i>Accipiter gentilis</i>	Male, 0.49–0.54 Female, 0.69–0.71	Male, 0.59 Female, 0.71	0.79–0.83	Kenward et al. (1999)
<i>A. nisus</i>	0.453 ± .071	0.626 ± 0.063	0.609 ± .054	Newton and Rothery (1997)
<i>Caracara cheriway</i>	0.694		0.919	Morrison (2003)
<i>Falco columbarius</i>	Female, 0.055 ± 0.012 Male, 0.23 ± 0.032		0.62 ± 0.11	Lieske et al. (2000)
<i>F. naumanni</i>	0.57 ± 0.05		0.67 ± 0.06	Prugnolle et al. (2003)
<i>F. peregrinus</i>	0.376 ± 0.076 0.54 ± 0.077	0.861 ± 0.066 0.670 ± 0.098	0.859 ± 0.025 0.800 ± 0.054	Kauffman et al. (2003) Craig et al. (2004)
<i>F. punctatus</i>	Varied annually		0.77 ± 0.02	Nicoll et al. (2004)
<i>Tyto alba</i>	0.172 ± 0.045		0.720 ± 0.044	Altwegg et al. (2003)

Rates are expressed as estimate ±SE.

of prey resources, familiarity with landscape features allowing hunting and defense efficacy, association with a cooperative hunting partner, and establishment of dominance over or mutual tolerance with other, potentially dangerous raptors.

Our apparent survival rate estimates are comparable to those obtained for other falcon populations and those of other raptors (Table 3). The three smaller falcon species for which survival rates have been estimated using methods comparable to ours show lower adult survival rates (Lieske et al., 2000; Prugnolle et al., 2003; Nicoll et al., 2004). However, for peregrine falcons (*Falco peregrinus*) in California, a Barker model mixing live recaptures, resightings, and dead recoveries produced mean survival rate estimates virtually identical to those calculated here for wild aplomado falcons (Kauffman et al., 2003). This is surprising, considering that the larger, cliff-nesting peregrine ought to have fewer predators than tree-nesting aplomado falcons sharing habitat with the great horned owl (*Bubo virginianus*), its principal predator (Jenny et al., 2004).

We could not find similar measures of breeding recruitment for other falcon species. Territoriality of breeding aplomado falcons, likely near saturation within our study area, actively prevents non-breeding falcons from acquiring a territory (Hunt, 1998). To do so, they must either eject the previous occupants or directly out-compete rivals for vacancies, possibly affected, in the case of wild versus hacked falcons, by developmental differences in socialization. These considerations may underlie the higher recruitment rate of wild falcons, advantaged, as they are, by parental association.

5. Conclusions

Our findings show that wild-reared descendants of captive-bred stock may exhibit very different attributes than the founding animals. Using mark-and-resighting analysis, we found evidence for differences in two important life history traits of wild and hacked aplomado falcons maturing in a common environment. Wild individuals survived and recruited at far higher rates. These results underscore the usefulness of frequent evaluation by project managers of the trend and composition of recovering populations, with the potentiality of adaptive redirection of project emphasis when indicated. By comparing the vital rates of groups within the population, we found that wild falcons dominated local replacement of breeders. Similar analyses earlier in the project cycle might have suggested an earlier management focus on factors influencing the fecundity of wild pairs.

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