

The genetic rescue of the Florida panther

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Abstract

We examine the consequences of panthers introduced from Texas into south Florida, an area housing a small, isolated, inbred and distinct subspecies (*Puma concolor coryi*). Once part of a continuous, widespread population, panthers became isolated in south Florida more than a century ago. Numbers declined and the occurrence of genetic defects increased. Hoping to reverse the genetic damage, managers introduced eight female panthers from Texas into south Florida in the mid-1990s. This action was highly controversial and we explain the arguments for and against the intervention. We synthesized data systematically collected on the Florida panthers from before, during and after this management intervention. These data include information on movements, breeding, mortality, survivorship and range. There is no evidence that purebred Florida females produce fewer kittens at a later age or less often than do hybrid cats (i.e. those with a Texas ancestor). Hybrid kittens have about a three times higher chance of becoming adults as do purebred ones. Hybrid adult females survive better than purebred females; there is no obvious difference between the males. Males die younger than females, are more often killed by other males and are more likely to disperse longer distances into habitats that are dangerous to them. Hybrids are expanding the known range of habitats panthers occupy and use.

Introduction

Will the introduction of genetically unrelated individuals into a small, isolated population reduce the genetic problems it likely suffers and so allow its numbers to increase? Human actions have forced small range and isolation on many populations, so whether to rescue them in this way is a pressing, practical question. It is also a controversial one. Rescues may inevitably fail and so waste resources better spent on other options. They may even harm the population. To address these controversies, we examine the consequences of cats introduced from Texas into south Florida, an area housing a small, isolated, inbred, and distinct subspecies (*Puma concolor coryi*).

The Florida panther once ranged across the south-eastern USA. Likely isolated from other panther populations for more than a century, fewer than 100 survive in south Florida (Maehr, 1997). The loss of habitat and the increasing proximity of human settlement and roads led to its protection by the state of Florida (in 1958) and listing as Federally Endangered (in 1967). Many individuals exhibited a high frequency of unique morphological characters and physiological abnormalities such as kinked tail and cowlick, sperm defects and heart defects (Roelke, Martenson & O'Brien,

1993). Instances of these defects increased as the population shrank (Sunquist & Sunquist, 2001). Some 90% of males born after 1990 had one or both testicles undescended, a condition not recorded before 1975.

In the Federal Register of March 28, 1991, the Fish and Wildlife Service announced its intent 'to evaluate a program designed to mix non-Florida panthers with Florida panthers for genetic enrichment purposes' (Pulliam, 1991). It noted its acceptance of an Environmental Assessment, prepared by D. B. Jordan, and circulated in draft form in June 1990 that had the release of cats from elsewhere as one of several options.

Subsequent workshops at the National Zoo in Washington, DC, in May 1991, and at White Oak Plantation, Florida, in October 1992 recommended the introduction of cats from the geographically nearest population in Texas, classified as *Puma concolor stanleyana*.

Subsequently, the Florida population increased its numbers and range. A conservation success story, perhaps, but experienced scientists offered an array of arguments to oppose the rescue (Maehr & Lacy, 2002). This case history examines those arguments, assembles data to justify our assertion that it was a success and asks what lessons can be learned from such a bitterly contested decision.

General arguments for and against rescue

To make a decision to rescue an inbred population by introducing individuals from outside it, one must evaluate a causal chain of actions. (1) Following human-caused range loss, there is (2) inbreeding in the resultant small population(s), (3) with a consequent increase in the proportion of genetically compromised individuals that causes (4) a decline in population growth rate (Frankham, Ballou & Briscoe, 1992). Rescue is an exciting management tool – it has the potential to prevent the population's extinction. The chain is logically compelling, so easy to embrace conceptually, and it provides a strong management choice to ameliorate 'inbreeding depression'. The chain is quite demanding to demonstrate, however.

A review (Pimm, 1991) at the time of the decision to rescue the Florida panther, cited Ballou & Ralls (1982), and Ralls, Ballou & Templeton (1988) as compelling evidence that the young of closely related, captive-bred mammals died in greater numbers than unrelated mammals.

Certainly, sufficiently small, isolated populations inevitably lose genetic variability through the shuffling of genes. The review, however, noted that only a few studies of wild vertebrates for which human actions had clearly reduced population size reported a consequent loss of genetic variability. A comparison of lion populations was one (Wildt *et al.*, 1987). Some studies of small populations found no obvious losses. The Indian rhinoceros *Rhinoceros unicornis* was such a study (Dinerstein & McCracken, 1990). Many studies inferred low population size and impending declines from low genetic variability without providing population data to support the association (Pimm *et al.*, 1989). A recent review (Frankham, in press) found a preponderance of comparative, field-based studies finding evidence for inbreeding, although the total number of studies was still relatively small.

Whether or not genetic difficulties diminish the population growth rates of wild species is not clear. It is altogether a much more difficult issue to demonstrate. For, even if one accepts the first three steps, the last one does not follow. Genetically handicapped individuals may have short lives and produce no heirs, but demonstrating this is not sufficient. For almost all populations, the majority of offspring die before reproducing. Trivially for a stable population, each pair produces a pair to produce the next pair (on average), while all the other young fail to do so. So, a species of cat that produces, for instance, 10 kittens over an individual female's lifetime should have only two of them survive to reproduce and the other eight die. The loss of inbred individuals may be part of this normal wastage of individuals – they may be in the eight that die. This is one end of a continuum, of course. The other end is that inbreeding does indeed cause an additional loss of individuals – more than eight individuals die – and that leads to the decline in population numbers.

Which circumstance obtains – and likely every natural situation will be somewhere in the middle – has important implications for those who manage species for which habitat loss has made them rare and isolated. Managers with limited

resources likely want something more than hypothetical possibilities before committing those resources.

At best, rescues of small, isolated populations may be an expensive solution that managers must repeat periodically to prevent inbreeding and the population declines posited to follow (Shields, 1993).

Worse, rescues may be simply wasted efforts – for the reasons outlined – that divert resources from more cost-effective interventions. Restoring or protecting more habitats or removing enemies may be better choices. The first question to ask of any managed introduction is whether there is unoccupied habitat in which the individuals might flourish. Habitat loss is overwhelmingly why most threatened species got that way. Thus, if a species has been lost from an area, or reduced to only a small population, by far the most parsimonious explanation is that a suitable, but unoccupied, habitat no longer exists, and so introductions will be a wasted effort. Clearly, enemies introduced from outside their native range threaten some species, in which case, the comparable question applies: are there suitable places for introductions that are free of those enemies?

Introductions may be directly harmful if the introduced individuals lack necessary adaptations that the native individuals possess (Shields, 1993). Those who claim that demographic harm might result from outbreeding with individuals from outside the local population have a similarly difficult burden of proof to those concerned about inbreeding. They often quote the same 50-year-old field study (Turcek, 1951) based on anecdotal observations of the failure of a demographic rescue of ibex *Capra ibex*. The hybrids gave birth to young at an inopportune time of year.

Finally, introductions may destroy the population's genetic distinctiveness, which might be the reason we deem it worthy of conservation.

The most compelling evidence for managers contemplating an introduction would be the success of other rescues. A recent example is Westemeier *et al.*'s (1998) rescue of the isolated prairie chicken *Tympanuchus cupido* population in Illinois. Other experiments of introducing individuals from outside small populations include work on the flower *Ipomopsis aggregata* in Arizona (Heschel & Paige, 1995) and on the adder *Vipera verus* in northern Europe (Madsen, Ujvari & Olsson, 2004). These show the benefits of added genetic diversity. The compendium of such direct studies is still so small that it provides scant support for managers justifying expensive rescues.

Specific arguments in the case of the Florida panthers

The arguments for introducing cats from elsewhere were made forcefully and they prevailed after extensive review and public comment. Nonetheless, concerns about this panther rescue were expressed with particular vigor. Maehr (1997) wrote: 'Genetically fortified kittens will soon be loosed upon a south Florida landscape that has repeatedly demonstrated its inability to nurture them'. Maehr and other opponents

cited the broad arguments already introduced, making them specific for this case and introduced new ones.

The first was that the remaining cats constituted a stable population that saturated the available usable space in south Florida (Maehr & Cox, 1995; Maehr, 1997). Maehr's papers never conceded that the population had declined to 30 cats, but claimed a population of 70 in the northern area, north of I75 and west of SR29, had saturated the landscape (see Fig. 3 for locations).

Moreover, there was the argument that the population might be increasing, following its more stringent protection. Maehr & Caddick (1995) reported an excess of births over deaths and first year kitten survival rates exceeding 80%, leading them to conclude that: '... the panther displays ... characteristics of an expanding population that appears unencumbered (for the present) by low genetic variability'.

An extension of this argument, Maehr and his colleagues supposed that this population – in contrast to other panthers – was a habitat specialist. This argument may be true, but can very easily be artifactual. Obviously, as populations shrink, they must occupy fewer habitats, therefore appearing more specialized. Moreover, studies of range shrinkage demonstrate that human actions typically force a species to retreat to what was once the edge of its range, apparently specializing in habitats that are not likely to be optimal (Channell & Lomolino, 2000).

Combined, these arguments broadly claimed that the panther was doing as well as it could in its very limited habitat, so adding cats would not improve that situation.

Next, there were concerns over outbreeding '... mating of individuals from normally allopatric populations may cause declines in fecundity or viability ... [it] can stem from genetic adaptation to the local environment' (Maehr & Caddick, 1995).

Finally, if one introduces cats from Texas into Florida, will their progeny still be the Florida panther and so still be deserving of protection as a Federally listed endangered species? The Fish and Wildlife Service determined that such individuals would still qualify before releasing the Texas cats (Federal Register, February 7, 1996, 61, p. 4709).

The release

Despite concerns, managers released eight Texas cats to locations across south Florida in 1995. Pairs of Texas females were released in close proximity to one another in four localities across the known range of extant Florida panthers. Five of the Texas females bred, producing a total of 20 kittens. We call all their descendents 'hybrids' and those without a Texas ancestor 'purebreds'. Hybrids include cats with Texas mothers and both purebred or hybrid fathers as well as hybrid mothers with either purebred or hybrid fathers. (The numbers of the different classes are too small to warrant a further splitting of the analyses to detect the consequences.) The purebreds may have received genes from South American cats released into south Florida in the 1960s (O'Brien *et al.*, 1990). (We cannot evaluate the effects of these genes either, except to note that any beneficial

effects would likely decrease the differences between the hybrids and the purebreds.) Two Texas cats were killed soon after release, three eventually died and the remaining three were removed in 2002 and 2003.

Methods

Synthesis of information from multiple sources

The most complex task was compiling data from disparate sources and assembling them into a framework to address the essential demographic questions. Initially, we compiled data from capture reports, annual genetics management and veterinary reports, and confirmed population reports compiled by the Florida Fish and Wildlife Conservation Commission (FWC), National Park and Fish and Wildlife Services ranging from the mid-1980s to present. We created a structured data table into which we inserted the relevant data from the disparate sources. As this paper completed its review process, we were able to cross-reference and update the information from Land *et al.* (2004).

Our structured data table is available as Supplementary Material Table S1 in the online version of this article. It contains information as follows, with all sources from Land *et al.* (2004). Cats receive an adult number (i.e. FP67) when captured as adults or a kitten number (i.e. K42) when given a microchip transponder while in their mother's den. Not all kittens are marked and some cats are first encountered only as adults. In this case, K42 became FP67. We extracted these data from appendix IV of Land *et al.* (2004). We know whether a cat is purebred or a hybrid from its date of birth (births before the Texas introductions must be purebreds), and explicit information in their tables 10 and 11 plus appendices II, IV and V. Obviously, the young of a hybrid is also a hybrid by our definition. We were unable to assign hybrid or purebred status to two females, FP78 and FP80, and 13 males, FP68, FP72, FP76, FP81, FP89, FP104, FP117, FP123, FP125, FP126, FP127, FP131 and FP132. Appendix II provides information on each cat's capture date and age at first capture. From these data, we estimated the date of birth. Appendix II also provides the date and cause of death. For our analyses, we also needed the date a cat was last known to be alive. Such data are more diffuse: we obtained them from tables 1, 2, 6, 7, 10. These tables record when researchers caught cats for various reasons – such as to take blood samples – or when they were found in their dens with kittens. When radios failed, we used the last known date in the radio location database (see below). Finally, appendices II, IV and V provide information on which females produced which kittens and their date of birth.

In calculating adult mortalities, we started the period of record when researchers first handled the cat and gave it its 'adult' number. The record ended when a cat died or on the date when it was last known to be alive. We can count only natural causes of death as being relevant to the comparison of death rates *or* we can count all deaths. The latter include (for example) cats hit by vehicles on roads. One argument is that

we should exclude unnatural hazards. The converse is that the purebreds are less fit in some way, and must compensate in ways that lead them to expose themselves to greater risks.

Within each of these two assumptions, we calculated maximum likelihood estimates based on a fixed monthly mortality, for all cats combined, males and females, hybrids versus purebreds, and the four separate classes. To choose the best model, we used statistics based on information theory. All statistical procedures involve a trade-off between model fit and model complexity. Complex models always fit better than simpler ones, but some of the variables may contribute little. Information-theory statistics consist of a single number, which is the sum of two parts. The first part is the 'lack of fit' measured by $-2\ln(L)$, where L is the likelihood of the model (with parameters fitted by the method of maximum likelihood). The second part is the 'penalty term', and this is where various statistics differ. The best-known information-based statistic is Aikake's information criterion (AIC), in which the penalty term is simply $2k$, where k is the number of free parameters in the model (Aikake, 1973). We used AICc, a form of the calculation that corrects for small sample sizes, although this correction barely alters the numbers obtained and does not alter the conclusion. The results appear as a table that lists the model, its parameters and the associated statistics that allowed us to choose the best model.

In addition, we also reviewed and mapped all known radiotelemetry locations and movements of collared cats through June 2003. We also mapped the movements of the purebred and hybrid cats. In doing so, we noted the position when first collared and noted the last known position (often where the cat died). The 'average position' is the mean of all recorded latitudes and the mean of all recorded longitudes.

Results

Comparison of purebred and hybrid survivorship

From kitten to adult

From 1992 onwards, researchers marked 118 purebred and 54 hybrid kittens. Of these, 13 purebreds and 20 hybrids survived long enough to receive an 'adult' number. (This usually meant the cat received a radio collar, but always meant that researchers handled the cat in some way.) Some kittens died before they left the den. The difference between purebreds and hybrids is highly significant (χ^2 test, $P < 0.001$), with the hybrids showing a better than three-fold advantage in survival. Johnson *et al.* (2001) noticed this difference, but did not analyze the data in detail. It would seem to be a most striking confirmation of benefits of the introduction of new genetic material, but we urge some caution. The details matter, for although the difference surely reflects a real hybrid advantage, the result has some uncertainty.

That uncertainty stems from the difficulty of finding all the kittens in a den. Some cats first appear in the record as adults. From 1992 onwards, when kittens first received microchips, 18 purebreds were known first as adults compared to the 118 that were first known as kittens. The comparable numbers for hybrids are nine known first as adults to 54 known as kittens. There are an additional 21 cats of unknown parentage first known as adults. It is *theoretically* possible that 157 purebred kittens (118 marked plus 18 first known as adults plus 21 cats of unknown parentage now assumed to be purebreds) produced 52 cats that survived to adulthood (the 13 known purebred survivors plus the 18 plus 21). This is a statistically vanishingly improbable scenario. It would require one of us (Bass) and other cat researchers to deliberately miss exactly those purebred kittens that would survive to adulthood and no others. Nonetheless, this absurd scenario indicates that the three-fold better survivorship of hybrids over purebreds might be somewhat reduced by the uncertainties attending marking kittens with transponders.

Adult survivorship

Whether one uses all causes of death or natural causes only, the overall monthly mortality is 1.5% (Table 1). Splitting by sex, males have higher mortalities than females. Splitting by origin, purebreds have higher mortalities than hybrids.

The best model, in each case, is the one that compared all males to all females (Table 1). However, Table 1 shows that it improves on the model that includes different mortalities for all four classes (males, females, purebreds and hybrids) by a very small amount. We have an a priori expectation that hybrids would do better and an explanation of why all young males do badly. In Fig. 1, therefore, we show the four mortalities separately.

The distance – henceforth 'dispersal' – that a cat moves between first capture and when it died depends on age, but in a direction counter to what we had expected. We expected that the longer a cat lived, the greater the distance it would travel, other things being equal. In fact, inspection of the data shows that the distance cats move *declines* with age on average. Our causal argument is wrong and the wrong way around. Dispersal determines how long cats live. Wide-ranging cats die young, and these are predominantly males (see Fig. 3). Seven male cats dispersed > 50 km and died before 6 years old (five of them before 3 years old). We show later that the mechanism is likely that long dispersals are into areas that bring cats into contact with humans and human-dominated landscapes. Likely, males that move long distances do so because they are excluded by competitively dominant, resident males. Not coincidentally, young males that do not disperse are often killed by other cats, most likely resident males.

Reproductive success of purebred and hybrid cats in south Florida

We summarized the lifetime production of the 11 purebred and 13 hybrid females known to have produced kittens since

Table 1. Estimated mortality rate (monthly) of panthers by varied demographics and causes of death

	Monthly mortalities				AICc value
<i>All causes of death</i>					
All cats similar	0.015				790
Males versus females	0.009 F		0.023 M		779 ^a
Hybrids versus purebreds	0.016 FL		0.010 HY		790
Sexes and origins differ	0.011 FL, F	0.005 H, F	0.023 FL, M	0.026 HY, M	780 ^b
<i>Natural deaths only</i>					
All cats similar	0.013				618
Males versus females	0.009 F		0.021 M		609 ^a
Hybrids versus purebreds	0.015 FL		0.008 HY		618
Sexes and origins differ	0.010 FL, F	0.005 HY, F	0.021 FL, M	0.0183 HY, M	612 ^b

^aIndicates best model.

^bSecond best model.

F, female; M, male; FL, purebred Florida cats; HY, cats with at least one Texas parent or ancestor; AICc, Akaike's information criterion calculation.

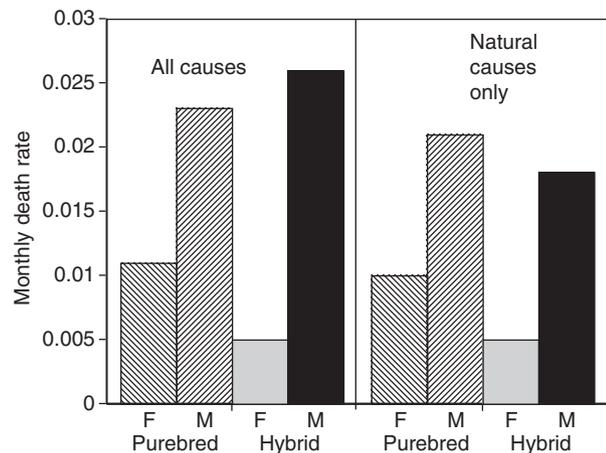


Figure 1 Monthly death rates of male (M) and female (F) cats that either have or do not have a Texas ancestor. Estimates either include all causes of death (left) or only natural causes (right). Hybrid females have the lowest mortality.

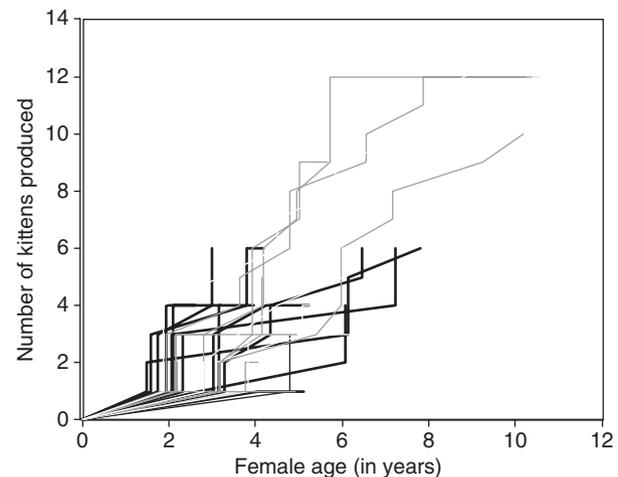


Figure 2 Cumulative number of offspring produced by females with age. Each line is an individual female: heavy black lines (bottom) are cats with a Texas ancestor, dashed gray lines (top) are purebred Florida cats.

the end of 1993. (The cats are purebreds numbers 48, 55, 56, 57, 69, 75, 101, 105, 106, 107, 112 and hybrids 61, 66, 70, 71, 73, 77, 83, 87, 88, 93, 95, 102, 110.) We excluded cats before this time because the data are almost certainly incomplete. Cat number FP48 was the first cat to have kittens given transponders.

Differences in fecundity might appear as differences in the age at first reproduction, the number of young produced in litter or the interval between litters. We combine these possibilities, by plotting the cumulative productions of kittens versus the female's age. Thus, each line in the figure represents one female: purebreds are shown with gray lines and are compared to hybrids with bold lines (Fig. 2).

In addition, we know of no offspring from three purebreds (numbers 49, 52 and 57) born in 1990, 1991 and 1992, respectively. These are old enough to have had kittens but

equally at a period when the data on production are less complete than in recent years. Two more recent purebreds (113 and 120) had young in April and January 2004, respectively. Likewise, we exclude eight hybrids (86, 91, 94, 103, 110, 116, 128 and 129) from the figure. While 110 and 116 have bred, the females in this set are too young to contribute much information on relative breeding success.

The conclusion is simple. There is no suggestion that the hybrid females produce more young, sooner, or more often than do purebreds.

Habitat, range use, interactions and movement

Before the introduction of Texas cats, most purebreds in south Florida were concentrated in an inverted 'L'-shaped

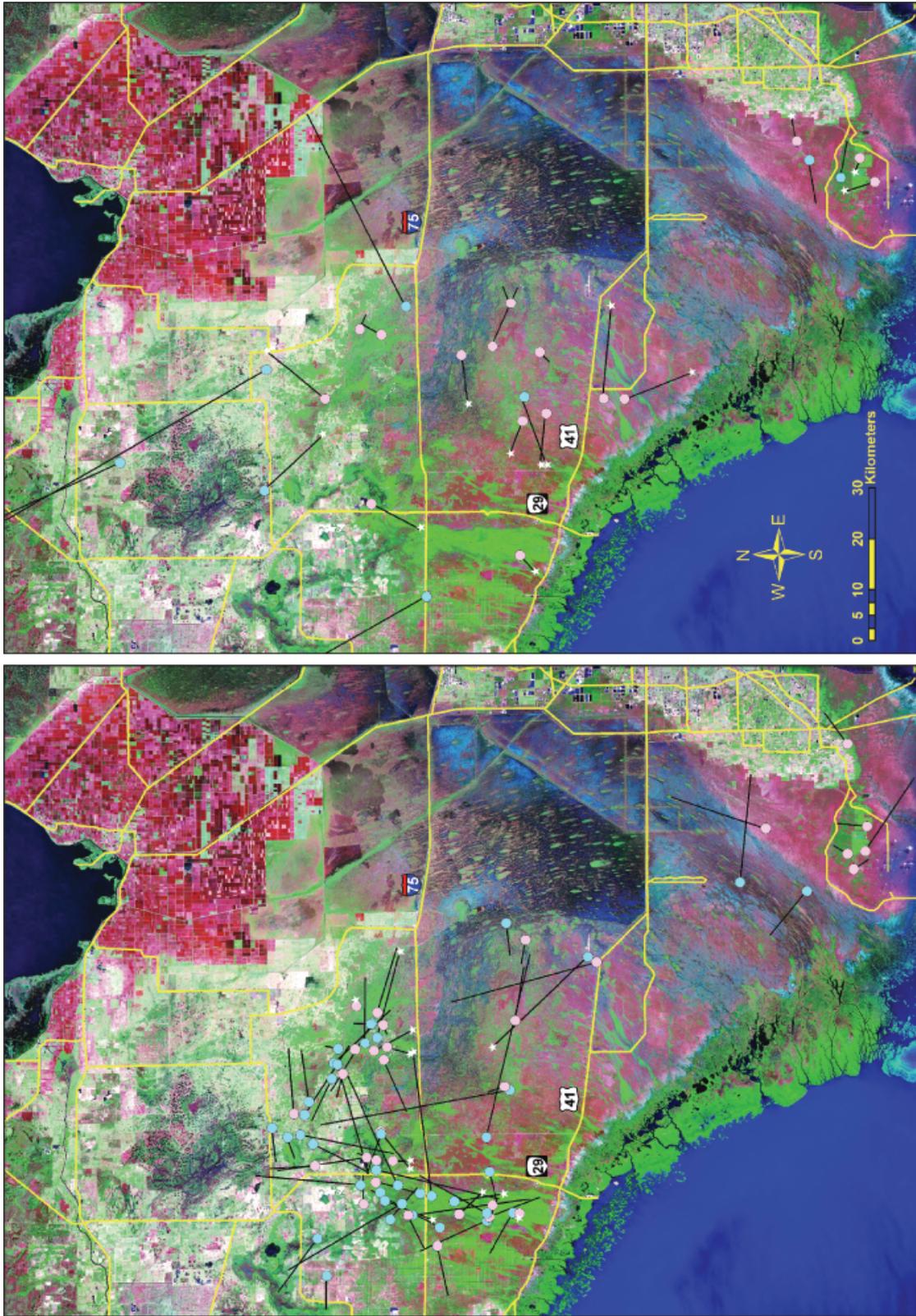


Figure 3 The area occupied by purebred cats (left) and Texas-born and hybrid cats (right). Blue symbols are male, pink ones are female. Lines connect the average position (●) determined by radiotelemetry to the positions last known (up to June 2003). Cats last known alive have stars at their terminus. The highways and interstate shown are those discussed in the text.

region. This region lies to the north of Interstate 75, then turning southwards of this road, west of State Highway 29, in a protected area that includes the Fakahatchee Strand State Preserve (Fig. 3). There were few purebreds south-east of this area, including all of Big Cypress National Preserve that lies south of Interstate 75 and Everglades National Park.

Figure 3 also shows the major human uses of the land. To the south-east of Lake Okeechobee lies an area of intense crop production that appears as a checkerboard (green areas are crops, reddish areas are fallow). On the other three sides, mixed crops, grazing and suburban development flank the lake; they show as lighter areas. To the immediate south of Lake Okeechobee lies the Everglades agricultural area (EAA), an area of intense production of sugar cane and other crops. Darker areas to the south of the EAA are a mix of cypress, pine and hardwood forests (green) and flooded marshes and prairies (blue). In the far south-west is a coastal strip of mangrove forest (bright green) and in the south-east, the southern extension of the urban areas of Miami and Homestead.

The data in Fig. 3 are the average of all the known locations derived from telemetry (colored dots) connected to the last known location. Stars at the line's end indicate that the cat was alive when last recorded.

The land uses shape the patterns of cat mortality. Cats, particularly males, that stray outside natural areas are often killed by cars. In addition, one purebred female was struck south of the city of Homestead and placed in captivity. Within the main cat area, – the L-shaped region – a common cause of male (and less often female) mortality is other cats. (Death from intraspecific aggression was significantly higher for males than for females (χ^2 test, $P = 0.009$.) Such cases of intraspecific aggression are determined by necropsy of the carcass, bite marks, etc. (Land *et al.*, 2004).

The four pairs of Texas introductions were (1) north of the Interstate, (2) in the Fakahatchee, (3) in Big Cypress south of the Interstate and (4) in Everglades National Park. As noted above, there was opposition to all these sites, the first two being in areas already well-populated by cats, the last two into areas deemed unsuitable. Of the first four cats, one was shot and another hit by a car, both dispersing into human-dominated landscapes. The other four cats introduced (into areas outside the main areas occupied by purebreds) produced the majority of the hybrids – those found south of Interstate 75 and east of Fakahatchee.

Discussion

In brief, we found that more than three times as many hybrid kittens appear to reach adulthood as do purebreds ones. Adult hybrid females have lower mortality rates than purebred ones. All surviving Texas and most of the hybrid cats have bred. During the years when the females were reproductively active, there were no differences in the cumulative numbers of young produced. Hybrid males have shorter lives than purebreds. Many were killed by what we assume are older, resident males, or because they disperse from these occupied places in others whether there are fewer cats but other dangers from human settlement.

As for the geography of the rescue, Maehr's (1997) concerns about introductions of cats into areas outside of their ranges in the late 1980s were clearly misplaced. Hybrid cats are beginning to expand their ranges to areas previously thought unsuitable.

In sum, collectively, there is a strong presumption that purebred cats suffer a variety of unfortunate demographic consequences that hybrid cats do not.

This rescue has increased the known cat population from ~30 (Robertson, Bass & McBride, 1985; US Fish and Wildlife Service, 1987) to the recent count of 87 (Shindle *et al.*, 2003). Cats now roam over a much larger area than in the past, including areas in the Everglades, Big Cypress and Fakahatchee once suggested to be unable to support them (Maehr, 1997). These areas involve mostly public lands that do not require private landowner concurrence for their management. This rescue does not guarantee the Florida panther's existence, but it has surely prolonged it.

Finally, what are the broader lessons from this case history? One is certainly that the issue is complex. The arguments for and against such introductions were – and still are – logically compelling. There are still only very few empirical studies such as this one to provide advice to managers. Equally, what science can deduce from a rescue when sample sizes are small (by force of circumstance) may also be difficult to interpret. As elsewhere, managers must often exercise conservation options under considerable uncertainty, something that only an increasing body of well-documented case histories can help reduce.

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References

- Aikaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In *Second international symposium on information theory*: 267–281. Petrov, B.N. & Csaki, F. (Eds). Budapest: Akademia Kiado.

- Ballou, J. & Ralls, K. (1982). Inbreeding and juvenile mortality in small populations of ungulates: a detailed analysis. *Biol. Conserv.* **24**, 239–272.
- Channell, R. & Lomolino, M.V. (2000). Dynamic biogeography and conservation of endangered species. *Nature* **403**, 84–86.
- Dinerstein, E. & McCracken, G.F. (1990). Endangered greater one-horned rhinoceros carry high levels of genetic variation. *Conserv. Biol.* **4**, 417–423.
- Frankham, R. (in press). Genetics and extinction. *Biol. Conserv.* (in press).
- Frankham, R., Ballou, J.D. & Briscoe, D.A. (1992). *Introduction to conservation genetics*. Cambridge, UK: Cambridge University Press.
- Heschel, M.S. & Paige, K.N. (1995). Inbreeding depression, environmental stress, and population size variation in scarlet gilia (*Ipomopsis aggregata*). *Conserv. Biol.* **9**, 126–133.
- Johnson, W.E., Eizirik, E., Roelke-Parker, M. & O'Brien, S.J. (2001). Applications of genetic concepts and molecular methods to carnivore conservation. In *Carnivore conservation*: 335–354. Gittleman, J.L., Funk, S.M., Macdonald, D. & Wayne, R.K. (Eds). Cambridge, UK: Cambridge University Press.
- Land, D., Shindle, D., Cunningham, M., Lotz, M. & Ferree, B. (2004) *Annual report: Florida panther genetic restoration and management*. US Fish and Wildlife Service, Naples, FL. Available at <http://www.panther.state.fl.us/news/reports.html>
- Madsen, T., Ujvari, B. & Olsson, M. (2004). Novel genes continue to enhance population growth in adders (*Vipera berus*). *Biol. Conserv.* **120**, 145–147.
- Maehr, D.S. (1997). *The Florida panther: life and death of a vanishing carnivore*. Washington, DC: Island Press.
- Maehr, D.S. & Caddick, G.B. (1995). Demographics and genetic introgression in the Florida panther. *Conserv. Biol.* **9**, 1295–1298.
- Maehr, D.S. & Cox, J.A. (1995). Landscape features and panthers in Florida. *Conserv. Biol.* **9**, 1008–1009.
- Maehr, D.S. & Lacy, R.C. (2002). Avoiding the lurking pitfalls in Florida panther recovery. *Wild. Soc. Bull.* **30**, 971–978.
- O'Brien, S.J., Roelke, M.E., Yuhki, N., Richards, K.W., Johnson, W.E., Franklin, W.L., Anderson, A.E., Bass, O.L., Belden, R.C. & Martin, J.S. (1990). Genetic introgression within the Florida panther *Felis concolor coryi*. *Natl. Geogr. Res.* **6**, 485–494.
- Pimm, S.L. (1991). *The balance of nature? Ecological issues in the conservation of species and communities*. Chicago: University of Chicago Press.
- Pimm, S.L., Gittleman, J., McCracken, G.F. & Gilpin, M. (1989). Genetic bottlenecks: alternative explanations for low genetic variability. *Trends Ecol. Evol.* **4**, 176–177.
- Pulliam, J.W. (1991). Federal Register, Thursday, March 28, 56: 12950–12952.
- Ralls, K., Ballou, J.D. & Templeton, A.R. (1988). Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conserv. Biol.* **2**, 185–193.
- Robertson, W. Jr, Bass, O. Jr & McBride, R.M. (1985). *Review of existing information of the Florida panther in EVER, BICY and environs with suggestions for need and research*. Unpublished technical report prepared for Superintendent, EVER, April 23, 1985.
- Roelke, M.E., Martenson, J. & O'Brien, S.J. (1993). The consequences of demographic reduction and genetic depletion in the endangered Florida panther. *Curr. Biol.* **3**, 340–350.
- Shields, W.M. (1993). The natural and unnatural history of inbreeding and outbreeding. In *The natural and unnatural history of inbreeding and outbreeding*: 143–173. Thornhill, N.W. (Ed.). Chicago, IL: University of Chicago Press.
- Shindle, D., Cunningham, M., Land, D., McBride, R. & Lotz, M., Ferree, D. (2003) *Annual report: Florida panther genetic restoration and management*. (US Fish and Wildlife Service, Naples, FL). Available at <http://www.panther.state.fl.us/news/reports.html>
- Sunquist, M.E. & Sunquist, F. (2001). Changing landscapes: consequences for carnivores. In *Carnivore conservation*: 399–418. Gittleman, J.L., Funk, S.M., Macdonald, D. & Wayne, R.K. (Eds). Cambridge, UK: Cambridge University Press.
- Turcek, F.J. (1951). Effect of introduction on two game populations in Czechoslovakia. *J. Wildl. Mgmt.* **15**, 113–114.
- US Fish & Wildlife Service (1987). *Florida panther (Felis concolor coryi) recovery plan*. Prepared by Florida Panther Interagency Committee for the US Fish and Wildlife Service, Atlanta, GA.
- Westemeier, R.L., Brawn, J.D., Simpson, S.A., Esker, T.L., Jansen, R.W., Walk, J.W., Kershner, E.L., Bouzat, J.L. & Paige, K.N. (1998). Tracking the long-term decline and recovery of an isolated population. *Science* **282**, 1695–1698.
- Wildt, D.E., Bush, M., Goodrowe, K.L., Packer, C., Pusey, A.E., Brown, J.L., Joslin, P. & O'Brien, S.J. (1987). Reproductive and genetic consequences of founding isolated lion populations. *Nature* **329**, 328–330.

Supplementary material

The following material is available for this article online: **Table S1**.

This material is available as part of the online article from <http://www.blackwell-synergy.com>