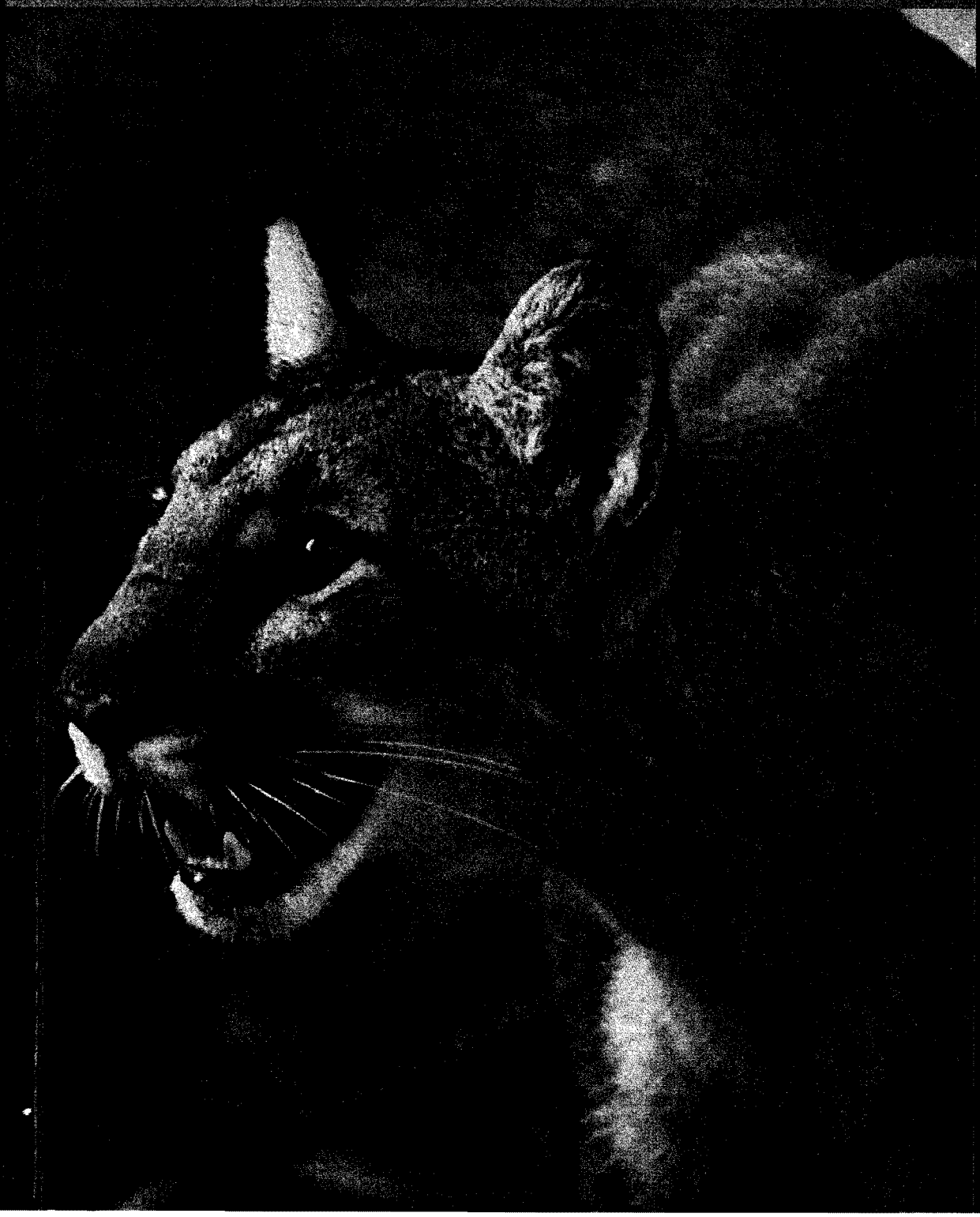
Animal Conservation

Volume 9 | May 2006 | Number 2



Quantitative studies for the conservation of populations, species and communities

Featured Paper and Commentaries: The Florida Panther. See pp. 113–134.

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Volume 9 Number 2 May 2006 Pages 113–236

Animal Conservation

CONTENTS



Front cover: Florida panther
Puma concolor coryi
Photo: Stuart Pimm

Featured Paper and Commentaries: The Florida Panther

The Florida panther: an editorial perspective
Cowlishaw, G., Crandall, K., Gittleman, J. L. and Milner-Gulland, E. J. 113

FEATURED PAPER

The genetic rescue of the Florida panther
Pimm, S. L., Dollar, L. and Bass, O. L. Jr 115

Response to article: 'The genetic rescue of the Florida panther' by Pimm *et al.* (2006)
Mills, M. G. L. 123

Recovery of the Florida panther – genetic rescue, demographic rescue, or both? Response to Pimm *et al.* (2006)
Creel, S. 125

Of cats and Haruspices*: genetic intervention in the Florida panther. Response to Pimm *et al.* (2006)
Maehr, D. S., Crowley, P., Cox, J. J., Lacki, M. J., Larkin, J. L., Hoctor, T. S., Harris, L. D. and Hall, P. M. 127

Ockham and Garp. Reply to Maehr *et al.*'s (2006) response to Pimm *et al.* (2006)
Pimm, S. L., Bass, O. L. Jr and Dollar, L. 133

Taxonomic selectivity in amphibians: ignorance, geography or biology?
Bielby, J., Cunningham, A. A. and Purvis, A. 135

Combining genetic and geospatial analyses to infer population extinction in mygalomorph spiders endemic to the Los Angeles region
Bond, J. E., Beamer, D. A., Lamb, T. and Hedin, M. 145

Breeding site selection by bearded vulture (*Gypaetus barbatus*) and Eurasian griffon (*Gyps fulvus*) in the Caucasus
Gavashelishvili, A. and McGrady, M. J. 159

Effect of salmonid introduction and other environmental characteristics on amphibian distribution and abundance in mountain lakes of northern Spain
Orizaola, G. and Braña, F. 171

Human–wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock
Michalski, F., Boulhosa, R. L. P., Faria, A. and Peres, C. A. 179

Impact of density-dependent nest destruction on emergence success of Guianan leatherback turtles (*Dermochelys coriacea*)
Caut, S., Hulin, V. and Girondot, M. 189

Abundance and distribution of the endangered loggerhead turtle in Spanish Mediterranean waters and the conservation implications
Gómez de Segura, A., Tomás, J., Pedraza, S. N., Crespo, E. A. and Raga, J. A. 199

Surveying bats for conservation: the status of cave-dwelling bats on Curaçao from 1993 to 2003
Petit, S., Rojer, A. and Pors, L. 207

Incorporating uncertainty in spatial structure for viability predictions: a case study of California sea lions (*Zalophus californianus californianus*)
Gonzalez-Suarez, M., McCluney, K. E., Aurioles, D. and Gerber, L. R. 219

Carotenoids, colour and conservation in an endangered passerine, the hihi or stitchbird (*Notiomystis cincta*)
Ewen, J. G., Surai, P., Stradi, R., Møller, A. P., Vittorio, B., Griffiths, R. and Armstrong, D. P. 229

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EDITORIAL

The Florida panther: an editorial perspective

G. Cowlishaw, K. Crandall, J. L. Gittleman & E. J. Milner-Gulland
Editors

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One of the most difficult questions in conservation science is when we as humans should intervene in natural ecological and evolutionary problems. Even when there are presumed successes, such as in bringing back populations from decline or ridding areas of invasive species, there is the feeling that we have not necessarily done the right thing – the natural process has to some extent been tampered with. Perhaps the hottest scientific topic in this regard is whether charismatic species (often carnivores) benefit genetically or ecologically when individuals from outside populations are introduced into declining ones. In this issue is a series of articles evaluating the successes, failures and contentious issues concerning introductions and consequent long-term management of the Florida panther. Because of the strong feelings aroused by this set of articles, we feel it is important to clarify the editorial process that took place.

The original manuscript by Pimm, Dollar & Bass (2006) was submitted on 28 September 2004. Accompanying the submission was an extensive cover letter explaining the context and history of the work, including a statement from Pimm acknowledging that the management of the Florida panther was controversial. Pimm stated that if *Animal Conservation* were to accept the paper, he would request that Dave Maehr, one of the principal researchers long involved with the panther issue, be sent the manuscript for comment. The manuscript was reviewed by two external referees. On 10 January 2005, the paper was rejected with encouragement to resubmit if the authors could respond thoroughly and effectively to the referees' comments. A revised manuscript was received on 16 April 2005. The paper was re-reviewed and acceptance was recommended following further revision.

The editors finally accepted the manuscript on 4 August 2005. We subsequently decided to select the paper as a 'featured article' and solicited invited replies from experts in the field (including David Maehr, Gus Mills, Scott Creel and others). Through the course of this process, concerns were raised about the provenance of the data used by Pimm *et al.* (2006), leading to a protracted series of reviews, commentaries and investigations. In the editorial office, we considered the extent to which Pimm *et al.* (2006) used only publicly accessible information (i.e. a government report by Land *et al.*, 2004) for their analyses. We satisfied ourselves that the information analyzed was appropriately gathered in a meta-analysis-type fashion; that is, individual animals, their relatedness and population structure could be gleaned from the databases publicly available. Following months of investigation, the editors concluded in January 2006 that the results were reliably based on data in the public domain. On this basis, we went ahead with the publication of the Pimm *et al.* (2006) paper.

Conservation science proceeds by examining new questions and collecting necessary information that will better inform whether panthers and other threatened species are more viable when we as humans do meddle. We hope that the publication of these papers will further this science by allowing others to effectively address these issues, both by verification and by extension.

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FEATURED PAPER

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.

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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

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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 Aikaike's information criterion (AIC), in which the penalty term is simply $2k$, where k is the number of free parameters in the model (Aikaike, 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

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

	Monthly mortalities				AICc value
All causes of death					
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]
Natural deaths only					
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]

[a]Indicates best model.
[b]Second best model.
F, female; M, male; FL, purebred Florida cats; HY, cats with at least one Texas parent or ancestor; AICc, Aikaike's information criterion calculation.

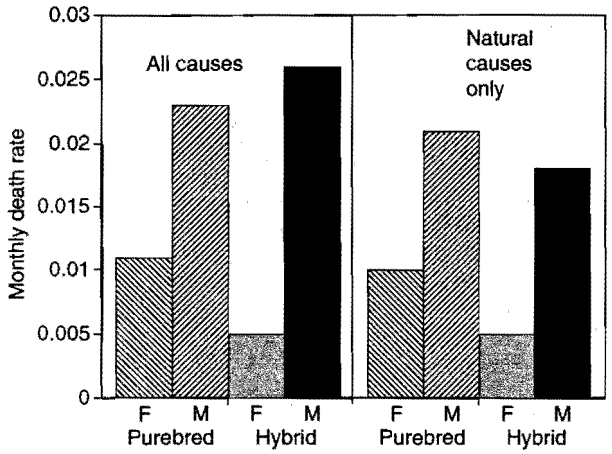


Figure 1 Monthly death rates of male (M) and female (F) cats that either have or do not have a Texas ancestor. Estimates either include all causes of death (left) or only natural causes (right). Hybrid females have the lowest mortality.

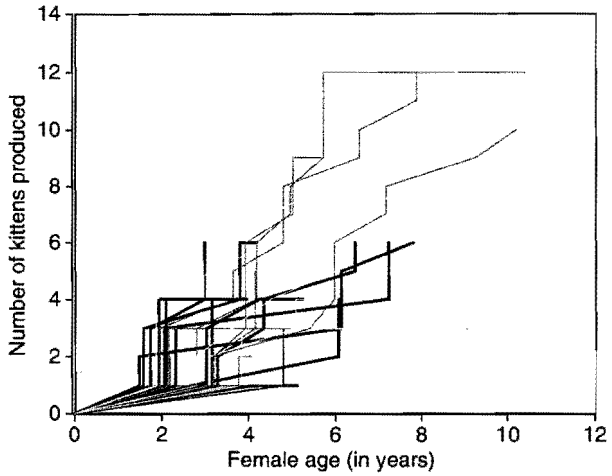


Figure 2 Cumulative number of offspring produced by females with age. Each line is an individual female: heavy black lines (bottom) are cats with a Texas ancestor, dashed gray lines (top) are purebred Florida cats.

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

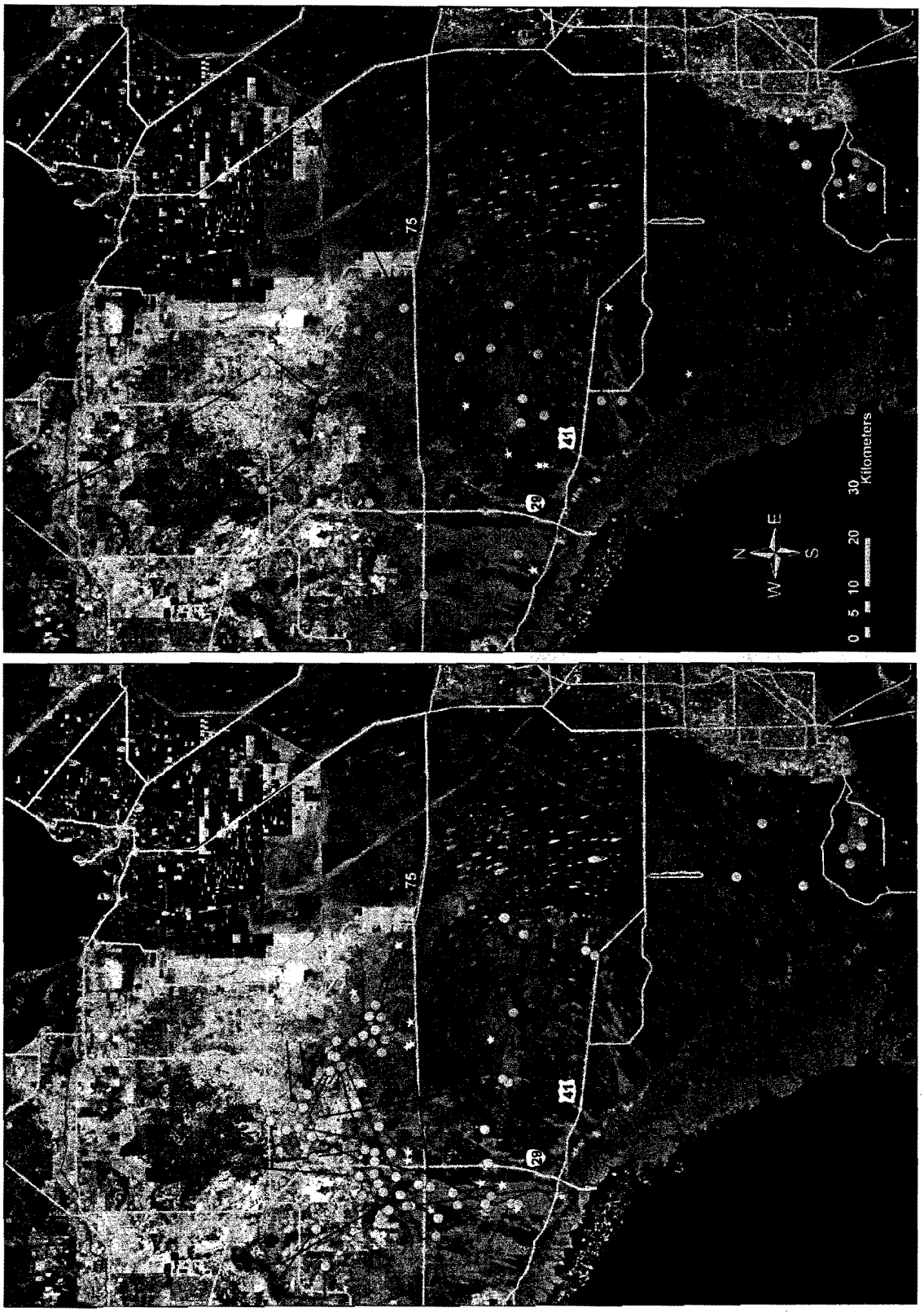


Figure 3 The area occupied by purebred cats (left) and Texas-born and hybrid cats (right). Blue symbols are male, pink ones are female. Lines connect the average position (•) determined by radiotelemetry to the positions last known (up to June 2003). Cats last known alive have stars at their terminus.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

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Response to article: 'The genetic rescue of the Florida panther' by Pimm *et al.* (2006)

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Florida panther; genetic intervention.

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This is a laudable attempt to measure the success of a controversial management action aimed at enriching the genetic integrity of a small population that has shown evidence of inbreeding depression. Much debate took place beforehand about the merits of this intervention. The results suggest that the operation was a success, at least in the short term, if the yardstick for success is better survival rates for hybrids than purebreds and an increase in the panther population from *c.* 30–87.

The fact that seemingly no clear research objectives or criteria to measure success were set at the beginning of the management action has made the extraction of relevant data difficult. The authors have done a good job in delving into all the bits and pieces of recorded information to extract what they could. These contortions of data extraction make the results somewhat difficult to follow, and this is not helped by the poorly presented table 1 (see Supplementary Material) and poorly captioned maps in fig. 3. To someone who does not know the area, it would have been helpful to mark and name on the map places such as Lake Okeechobee, the Everglades Agricultural Area and the Fakahathchee instead of lengthy explanations in the text.

As the authors point out, small samples and difficulties in obtaining relevant data from such a cryptic species make it hard to understand the underlying dynamics of this issue. For example, why are hybrids expanding into new habitats? Why were the purebreds unable to do this? Also, why were Big Cypress and Everglades National Park deemed unsuitable for panthers? Was it changes in conditions or the superior fitness of the hybrids that allowed them to colonize these areas?

In spite of the results, the authors readily concede that this does not prove that it is always advantageous and necessary to intervene. They seem to advocate more such interventions before we are in a position to provide advice to managers. Equally, there are examples of highly inbred populations persisting without intervention (again at least in the short term), for example Isle Royale wolves (Vucetich & Peterson, 2004), and of others even booming from a founder population of five to over 3000, for example Marion Island cats (van Aarde, 1986). More examples of what will happen with and without intervention are needed. It will obviously take a long time before enough empirical studies involving both experimental and control conditions are documented to fully understand if, when and how to intervene in the genetic management of small populations.

Be that as it may, how do you weigh the costs and benefits of operations of this nature in an overall conservation framework? Is this another example of society promoting a high profile and expensive operation on a charismatic species or subspecies – which in fact may not be as distinct from other subspecies of the puma as was once thought (Culver *et al.*, 2000) – in an area where the long-term viability of the species, because of high human pressure and development, must be in doubt? Odling-Smee (2005) argues that conservationists should concentrate on the importance of ecosystems to people and the services they provide to humankind as promoted in the United Nations sponsored Millennium Ecosystem Assessment. However, losing sight of the ethical and spiritual dimensions to conservation is unacceptable to many. Then there is also the very popular concept of concentrating on conserving biodiversity hotspots and the equally popular, labour-intensive and relatively expensive efforts of saving and rehabilitating orphaned, injured and captive-raised animals. We need to study, think about and discuss in more detail the relative merits of saving the lives of individual animals, species conservation, maintenance of biodiversity hotspots, and preservation of important ecosystems to humans, and how and where to divide and invest our scarce resources for best results. No easy task, given the diversity of opinions and agendas of our species.

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Recovery of the Florida panther – genetic rescue, demographic rescue, or both? Response to Pimm *et al.* (2006)

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Keywords
Florida panther; *Felis concolor*; survival; inbreeding; hybridization.

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Pimm, Dollar & Bass (2006) address difficult issues in their evaluation of the release of Texas panthers to mingle with the last 30 Florida panthers. This release was almost unique, because it was designed to let a hybrid swarm (Allendorf *et al.*, 2001) swamp a population that was genetically unique, but inbred. Trading off against this loss of unique evolutionary potential is, hopefully, a reduction of inbreeding depression that improves the population's demography and dynamics.

It is this benefit ('genetic rescue') that Pimm *et al.* (2006) seek to demonstrate, but the issue is more complex than it first appears. Intuitively, the population's growth from ~30 to 87 cats seems to resolve the question, but we should consider the possibility that population growth was because of simple demographic rescue rather than genetic effects. As shown by the restoration of wolves to Yellowstone (Smith *et al.*, 2003), small introductions of carnivores can produce dramatic population growth in cases where the initial population size was zero, which removes genetic rescue from consideration. The release of 31 wolves yielded a greater than fourfold increase in 5 years, substantially faster growth than the panthers have shown. Pimm *et al.* (2006) also note that 'hybrid cats are beginning to expand their ranges to areas previously thought unsuitable', but a growing population will often expand into new habitats, so this response may also be demographically driven.

To test for genetic rescue more directly, Pimm *et al.* (2006) compare the survival and reproduction of purebred and hybrid panthers. They conclude that there is 'a strong presumption that purebred cats suffer a variety of unfortunate demographic consequences that hybrid cats do not'. While I tend to agree that a reduction in inbreeding depression has probably played a role in the recovery, I am not certain. One obvious problem is that the demographic data from hybrids and purebreds come from different (although overlapping) periods, and carnivore populations (particularly small ones) often show marked temporal variation in survival and reproduction. A second problem is that differences in the age distribution of hybrids and purebreds are not considered in the analysis of adult survival.

Of greater concern to me is the equivocal evidence that reproduction and survival differ for adult hybrids and purebreds. Pimm *et al.*'s (2006) conclusion quoted above focuses on the observations that hybrids survive better among kittens and females, but it is important to recall that reproduction and adult male survival showed no benefit of hybridization. Consider the analysis of adult survival. The simple fact is that a model allowing for differences between purebreds and hybrids is no better than a model that ignores genetic differences. Pimm *et al.* (2006) state: 'Splitting by origin, purebreds have higher mortalities than hybrids.' But the data give no support to this statement, because models including and ignoring genetic differences are identically 11 Akaike's information criterion (AICc) units worse than the best model. Sex, on the other hand, is a good predictor of annual survival (11 AICc units better than the model accounting for genetic origin). A model that allows genetic origin to modify sex differences is not demonstrably worse than one allowing only for sex differences (1 AICc unit worse, where ΔAICc = 2 would indicate that genetic origin contributes no additional information; restricted to natural deaths, adding genetic origin substantially weakens the model allowing for sex differences: ΔAICc = 3). If these data had been presented as a factorial ANOVA, it would show that the main effect of genetic origin on survival was very weak. The information presented does not allow me to say whether the interaction of sex by origin would be significant, because no test statistics were reported and their fig. 2 does not include estimates of error for mean survival rates. At best, Pimm *et al.* (2006) are treating a significant interaction as though it was a significant main effect.

This precludes clean inferences about the effect of genetic rescue on adult survival. If we had data only for females, we would conclude that hybrids survive better. If we had data only for males, we would conclude the opposite. It seems

unlikely that this pattern would have been predicted a priori in formulating hypotheses about genetic rescue. Comparing data on natural deaths and deaths of all causes (their fig. 2a and b), we see another change in the sign of the effect (for males in this case). When the sign of an effect flip-flops repeatedly and unpredictably, cautious conclusions are in order.

With equivocal effects on reproduction and adult survival, but relatively clear effects on juvenile survival, it seems likely that reduced inbreeding has helped the population recover. The recovery itself is clear, but I do not think that the relative strengths of demographic and genetic rescue have been resolved. From the perspective of local ecology, increasing panther density and range expansion are clear successes. From the perspective of maintaining evolutionarily unique populations, this success comes at the cost of genetic swamping.

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Of cats and Haruspices*: genetic intervention in the Florida panther. Response to Pimm *et al.* (2006)

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Florida panther; *Puma concolor coryi*; genetic augmentation; social structure; habitat variability.

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*Plural of Haruspex, 'A Roman priest who practiced divination by the inspection of the entrails of animals' (Morris, 1969).

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Abstract

The claim that the Florida panther *Puma concolor coryi* has been genetically rescued by the introduction of Texas cougars *P. c. stanleyana* is based on the questionable development and interpretation of a maximum likelihood model, data dredging and a misleading presentation of historical data. In addition, the claim that Florida panther 'hybrids are expanding the known range of habitats panthers occupy and use' is offered in the absence of data or supporting analyses. By (1) ignoring regional differences in habitat quality, (2) ignoring the earlier extinction of the hybrid Everglades population, (3) ignoring the influence of social structure on the relative success of Texas cougars and their offspring, (4) using cursory spatial analyses of panthers before and after intervention and (5) choosing a second-best model, a misleading scenario was presented. Undoubtedly hybrid animals have increased in abundance and distribution on the south Florida landscape, but it is quite possible that current patterns of abundance and distribution would be similar if purebred Florida panthers had been introduced instead of Texas cougars in 1995. This is because all the demographic events that have occurred since genetic intervention in 1995 can be more reasonably explained by factors relating to panther social structure and habitat variability. We are hopeful that the current genetic management effort will contribute to the recovery of this endangered population; however, it is too early to claim that this intervention has succeeded or failed. We suggest a number of ways in which more reliable insight on this issue might be obtained.

Introduction

Announcement of the 'genetic rescue' of the Florida panther *Puma concolor coryi* was met with great fanfare in popular and technical science literature (e.g. von Bubnoff, 2005; Kleiner, 2005; Stokstad, 2005), despite the warnings of Tallmon, Luikart & Waples (2004) that the determination of such an outcome is fraught with difficulty. We recognize the efforts of Pimm, Dollar & Bass (2006) in highlighting the unfolding effort to manage the Florida panther through genetic intervention. But their interpretation of a subset of the limited data currently available is premature and speculative, and may actually undercut the recovery of this endangered population. (We prefer 'intervention' to 'rescue,' as the latter term prejudges an outcome that is yet to be determined.) Because it is of great interest to the conservation community, the progress of panther recovery must be thoroughly and carefully examined using historical, statistical and ecological information. The Pimm *et al.* (2006) paper contains several errors, but the most serious are those related to the development and interpretation of a maximum likelihood model, the absence of credible spatial analyses, and misleading demographic and ecological information. In addition, the paper does not examine multiple gene loci over multiple generations – the key to understanding change in population fitness (Tallmon *et al.*, 2004). Here we examine the Pimm *et al.* (2006) analysis, and then offer specific suggestions on how the implications of the intervention might be evaluated rigorously.

Shortcomings of the model

It is difficult to take data from various sources, gathered in various ways, and perform analyses capable of unambiguous interpretation. Unfortunately, none of the analyses presented in Pimm *et al.* (2006) are described adequately for thorough evaluation by a critical reader, except possibly the initial statistical test result comparing purebred and hybrid

survival from kitten to adult. If we suspend the skepticism appropriately associated with the mixture of sources and methods, and with unfulfilled statistical assumptions, a χ^2 test (*not* a 'c^2 test,' as stated in the paper) superficially suggests higher survival to recapture as an adult among hybrid cats than purebred cats – at least when 20 survivors to adult from 54 hybrid kittens are compared with 13 survivors to adult from 118 purebred kittens ($\chi^2 = 16.18$, $P<0.001$, 1 d.f.). But the genetically distinguishable adults first captured as kittens represent only 33 of the 81 adult animals captured. The authors note that 27 of the animals first captured as adults are genetically distinguishable, including nine hybrids and 18 purebreds. Oddly, they failed to mention that the ratio of hybrid to purebred adults in this group is essentially identical to the ratio of 54 hybrids to 118 purebreds among captured kittens ($\chi^2 = 0.04$, $P>0.5$, 1 d.f.). This means the 9:18 ratio of first-captured adults is consistent with equal survival from kitten to adult for purebreds and hybrids among these animals, and clearly fails to corroborate the result based only on recaptured animals. We believe this should leave the reader with considerably more doubt about genetically based survival differences than the authors conclude.

Equally unconvincing is the maximum likelihood analysis of adult survival and its interpretation. No rationale is provided for the lack of classical hypothesis testing, and the means of estimating the mortalities from the original data are not described. Here, we find the authors' logic to be circular in choosing a particular model over another, simply because it fit their expectations.

Pimm *et al.* (2006) appeared to use the Akaike information criterion (AIC) to evaluate a series of competing hypotheses that reflect plausible alternatives to a biological pattern of interest (Anderson & Burnham, 2002), in this case performance differences between hybrid and purebred panthers. However, in each group of maximum likelihood models analyzed by Pimm *et al.* (2006), the top two had $\Delta_i<4$, suggesting that both models have substantial support and are plausible (Burnham & Anderson, 1998). They also committed an error of omission (Guthery *et al.*, 2005) by not adequately interpreting all plausible models, while ignoring others that were 'almost' equally plausible. The AIC analysis thus provided no basis for either accepting or rejecting a difference in survival between hybrid and purebred adults.

Misleading identities

The Pimm *et al.* (2006) paper hinges on comparisons between so-called 'purebred' and 'hybrid' panthers, but underplays the fact that all known animals living in the Everglades (a sedge-and-grass-dominated system in south-eastern Florida) before genetic intervention in 1995 were hybrids. They acknowledge that this 'would likely decrease the differences between the hybrids and the purebreds,' but proceed with their analysis without considering the fact further. Culver *et al.* (2000) excluded these animals from an examination of ancestry in the species because O'Brien *et al.* (1990) and Roelke, Martenson & O'Brien (1993) recognized their South American ancestry based on the existence of a characteristic polymorphic allozyme locus (APRT). These animals likely resulted from captive-raised hybrid cougars that were released in Everglades National Park between 1957 and 1967 (Vanas, 1976; O'Brien *et al.*, 1990). Thus, the animal struck by a car near Homestead, Florida (presumably panther #21; Bass, 1994), is not evidence of higher vulnerability to 'unfortunate demographic consequences' among purebred panthers. Rather, it illustrates the risk to panthers, regardless of provenance, that live near roads and occasionally cross them. It should not be surprising that mortality among purebreds – especially males – is higher than that of hybrids. As is clear in the maps of Pimm *et al.* (2006), most hybrids inhabit areas that are relatively far from roads and human habitation.

Are genetic, demographic and spatial effects confounded?

Pimm *et al.* (2006) assert without evidence that habitat use is expanding into areas previously thought unsuitable. Elsewhere they claim that grasslands are used more by hybrids (Stokstad, 2005). Their map of points and lines is only a vague representation of spatial relations, yet most of these marks are centered in the north-western forested portion of panther range, where most of the animals are purebreds, and where panther numbers have been stable or increasing since the early 1980s.

The prognosis for continued panther occupation in the Everglades and other marsh-dominated landscapes is not good because of periodic high water conditions and relatively low prey densities (McCown *et al.*, 1991; Maehr & Lacy, 2002). This is the landscape where the recent (*c.* 1990) hybrid extinctions occurred (Bass & Maehr, 1991), and where the number of occupied panther home ranges steadily declined from the late 1980s through 2003 despite the 1995 introduction of Texas cougars (Cox, Maehr & Larkin, in press). Few terrestrial landscapes in south-eastern US reach the hydroperiodical extremes of the Everglades, where several endangered wetland-dependent species (e.g. wood stork *Mycteria americana* and snail kite *Rostrhamus sociabilis*) are adapted either to annual drying cycles or to extended wet periods (Harris *et al.*, 1996). The former hybrid population required three decades to go extinct – challenged by exposure to mercury (Roelke *et al.*, 1992, 1993) through consumption of bioaccumulating alternative prey species, such as the raccoon *Procyon lotor* and American alligator *Alligator mississippiensis* (Dalrymple & Bass, 1996). Mercury is still a concern for panthers living in this system (Land *et al.*, 2004). Prey species in the more productive, northwestern portion of the panther range are mostly not bioaccumulating primary consumers: the white-tailed deer *Odocoileus virginianus* and wild hog *Sus scrofa* (Maehr *et al.*, 1990).

The dots and lines in fig. 3 of Pimm *et al.* (2006) actually tell a different story than the offered interpretation. The attainment of a home range is a process fraught with challenges that are multiplied when colonizers (even if they

were translocated Texas cougars) attempt to establish in areas with an existing population. As Maehr & Lacy (2002) suggested, the most successful introduced Texas females were advantaged by being placed in areas where few panthers held land tenure. Elsewhere, hybrids may have avoided or were forced out of the L-shaped area that supported a dense purebred population upon their arrival, and where purebred residents had 'prior rights' (land tenure) to territories (Seidensticker *et al.*, 1973, p. 53). It indicates that 'no displacement of Florida panthers occurred and no disruptions to the existing social structure were observed' following the introduction of Texas cougars (Land *et al.*, 2004, p. 11). This suggests that hybrids have had some difficulty penetrating areas that were occupied by resident purebreds. If conditions in the Everglades and environs are currently supportive of panthers, as suggested by Maehr & Lacy (2002), then hybrids should prosper there because existing panther densities were low. Given that *Puma concolor* females tend to be philopatric (Maehr *et al.*, 2002), we should not expect purebred females to re-occupy the vacant or low-density range in only one or two generations. Under natural circumstances this is a gradual process, not one that comes about virtually overnight. While it may be true that 'most of the hybrid cats have bred' (Pimm *et al.*, 2006), it is important that they bred in areas that may not remain suitable habitat indefinitely (see Maehr & Lacy, 2002).

Current versus pre-1995 distribution

Pimm *et al.* (2006) use one-dimensional figures (dots and lines) to illustrate a two-dimensional analytical challenge; that is, where do modern panthers live? The most that can be said based on their map is that the current (but perhaps temporary) distribution of hybrids seems mainly to reflect where they were born. The figures tell us nothing about the spatial demands of individuals or the population, except that Texas females and hybrids have had a difficult time colonizing the core habitat. Texas cougars were moved thousands of kilometers as adults and then had kittens if conditions allowed. Alternatively, we examined radio-telemetry data (Florida Fish and Wildlife Conservation Commission) from 1981 to 2003, including 60 959 locations of 121 Florida panthers (including hybrids) and 5956 locations of the eight female Texas cougars introduced in 1995 (Land & Lacy, 2000). We excluded from our analyses location data of panthers <18 months of age because of potential biases in space use (i.e. their locations would be subsets of their mothers'), and individuals with <25 locations. These data contained 51 525 locations of 109 panthers (54F, 55M) divided between pre-introduction (1981–March 1995; 25F, 29M) and post-introduction (April 1995–2003; 41F, 32M). Eighteen panthers (12F, 6M) overlapped both time periods. We used Biotas 1.03a (Ecological Software Solutions, Urnäsch, Switzerland) to estimate panther distribution for each time period by generating 50, 95 and 99% fixed kernels using all telemetry locations within each period, recognizing that individuals with high numbers of locations can influence utilization distributions used to estimate range (most likely an issue in the Everglades where telemetry data have been collected more frequently). The 50% fixed kernel area is instructive for pointing out activity centers (e.g. Dickson & Beier, 2002; Atwood, Weeks & Gehring, 2004) and core areas (Kernohan, Gitzen & Millspaugh, 2001). We followed this with a more conservative analysis of adult female distribution (the true measure of range expansion) using arithmetic means of coordinate data to generate 50 and 95% fixed kernels for each time period. This allowed us to focus on the basic family unit as an index to breeding range and to reduce bias caused by over-representation of data from some individuals. In addition, we calculated and plotted the average geographic coordinate for each male.

The results (Fig. 1) indicate changes in the distribution of panthers between periods, but do not support the assertion of range expansion (the occupied range appears to have both waxed and waned, depending on geographic focus). Figure 1 confirms that the core (50% contour) of panther distribution remains in the north-west portion of the panther range, and that the overall distribution has become segmented since 1995. The 99% kernel actually indicates a range reduction of 273 km^2 after 1995. When just female panthers are examined (Fig. 2), the separation between the Everglades and the rest of panther range is evident, and the

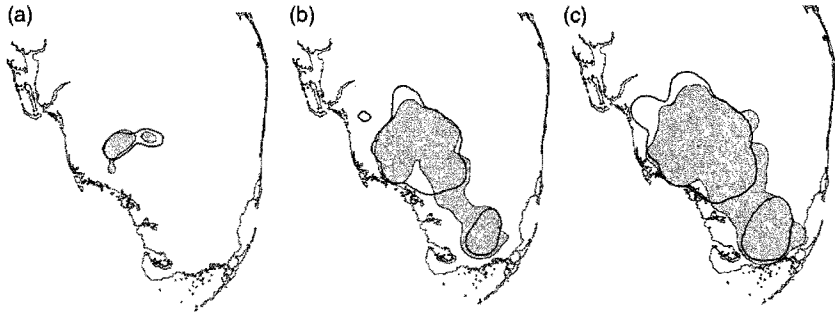


Figure 1 Distribution of Florida panther radio locations before (gray shading) and after (black outline) the introduction of eight Texas cougar females into south Florida in 1995. Contours represent (a) 50%, (b) 95% and (c) 99% fixed kernel areas. Note that pre-intervention distribution plots exhibited a continuous distribution at the 95 and 99% levels, whereas post-intervention areas are segmented.

clustering of adult females in the north-west is obvious. Post-intervention reductions of 681 and 2324 km^2 (50 and 95% fixed kernel, respectively) for females support the impression that suitable breeding range in south Florida is limited (Fig. 2). The distribution of males supports the observation that dispersal from breeding areas has increased since 1995 (Maehr *et al.*, 2002), except in the area between the Everglades and Big Cypress Swamp. We do not suggest that the amount of panther habitat has actually declined since 1995, but that habitat quality and its distribution in south Florida are dynamic, especially in south-eastern Florida. Such variation could be related to prey density and water levels, especially in the periphery of occupied range. Regardless, *Puma concolor* range expansion in south Florida has not occurred since 1995: the only cases that can be made are (1) the population is using a similar total area and (2) adult females may be using less area.

Population growth

Some introduced large mammals 'follow a pattern of adjustment to the new environment which consists of a single eruptive event' (Riney, 1964, p. 261). Such escape from natural controls is well known among insects and is usually temporary (Odum, 1971). The introduction of the Texas cougar into south Florida may be analogous to the introduction of the Himalayan tahr *Hemitragus jemlahicus* in New Zealand (Caughley, 1970) insofar as individuals of both populations were moved long distances to conditions that were different from their origins; both groups of introduced animals reproduced well where conspecific competition was low or absent. Such rapid establishment can result in 'large-scale die-offs, especially in years when some element of the habitat becomes especially critical, as in drought years' (Riney, 1964, p. 265). (Recurrent flooding that leads to prey declines, nutritional stress and increased susceptibility to disease is the likely threat to panthers living in south-eastern Florida.) The population then oscillates with reduced amplitude around carrying capacity.

The post-intervention panther population is still likely adjusting to increased density. Interestingly, six recent deaths in the northern area of the Big Cypress Swamp (Land *et al.*, 2004) may represent part of a post-eruption adjustment. These panthers (FP118, UCFP55, UCFP56, UCFP57, FP73 and FP77) died between April and July 2003 in the vicinity of the Big Cypress Seminole Indian Reservation. At least one was a Texas hybrid and two others may have been offspring of non-Florida escaped captives (inferred from Land *et al.*, 2004). Although a cause for these possibly natural deaths has not been released, the involvement of hybrid animals argues against the notion of genetic rescue in the Florida panther. Rather, like the long-distance dispersal events that occurred following Texas cougar introduction (Maehr *et al.*, 2002), such unprecedented mortality may simply be a density-dependent response by a population artificially and temporarily pushed above saturation density.

Pimm *et al.* (2006) inexplicably use a 1987 baseline population of 30 (8 years prior to genetic intervention), and incorrectly characterize the population estimate (74) of Maehr, Roof & Land (1991), which was an extrapolation based on a minimum density in a portion of panther range: not a range-wide census of animals documented by capture or spoor. From the beginning of panther radio telemetry in the early 1980s (Belden *et al.*, 1988), there has been a gradual increase in the number of animals under study. From the early 1980s through 2003, the number of known panther home ranges increased in the Big Cypress region of south-west Florida (Cox *et al.*, in press) through consistent annual capture efforts (essentially January–March prior to 1995). Some of this increase was because of the study of larger areas (Maehr *et al.*, 1991), but also because of the gradual dispersal of females into a vacant range. An

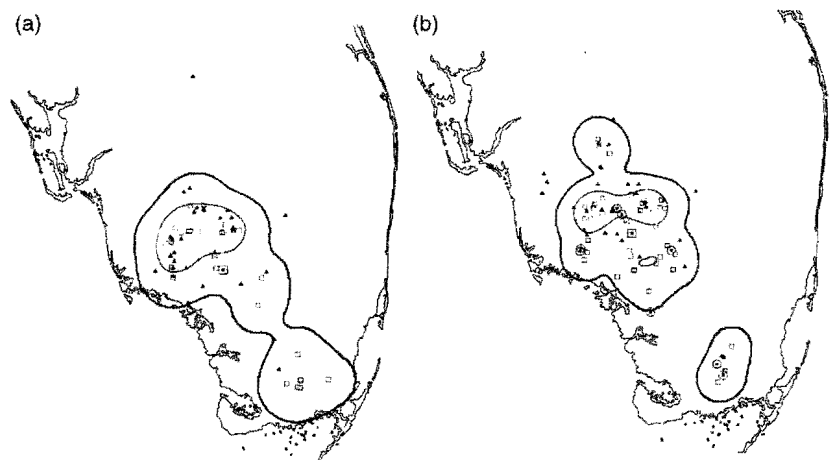


Figure 2 Fifty (shaded) and 95% fixed kernel areas before (a) and after (b) the introduction of eight Texas female cougars into south Florida in 1995, based on the arithmetic mean locations of all female panthers. Open squares and triangles represent the arithmetic mean location of individual female and male panthers, respectively. The dotted square represents the overall arithmetic center of all females, and the star represents the arithmetic mean location for all panthers. Circles with dots (b) represent the approximate release sites of Texas cougars.

example of this was the *c.* 10 km northward movement from her natal range and subsequent reproduction of purebred female #52 in 1992–1993 to an area that was formerly unoccupied (Maehr, 1996).

Policy missteps

Finally, the authors make a dangerous suggestion that the primary difference between public lands and others is that the former 'do not require private landowner concurrence for their management' (Pimm *et al.*, 2006). This statement, when taken with other premature claims that Everglades National Park and parts of Big Cypress National Preserve support 'thriving' panther populations (e.g. Comiskey *et al.*, 2002), engenders a perception among popular and regulation-enforcement onlookers that the need for private land conservation and management is somehow mitigated (Maehr, Larkin & Cox, 2004). Even worse, it flies in the face of programming to increase incentives for habitat and panther conservation on private lands, which, ultimately, are the only hope for longer term panther conservation in Florida (Maehr, 1990; Hoctor, Carr & Zwick, 2000; Maehr *et al.*, 2002). A diminution of conservation efforts on private land could threaten the existence and functionality of key habitats and dispersal corridors that occur nowhere else (Maehr, 1990). If anything, recognition of the ephemeral nature of some panther landscapes in south-eastern Florida should encourage the expansion of efforts to protect more habitat elsewhere.

Conclusion

Our main concerns about the Pimm *et al.* (2006) article stem from premature conclusions drawn from an inadequate analysis and inadequate explanations for how the conclusions were reached. Its data analyses and interpretations are selective, problematic and insufficient for attributing the panther's current demographic status to genetic intervention. Indeed, as Tallmon *et al.* (2004) observed, environmental, demographic and behavioral factors are central to understanding the effects of migration among small populations. Thus, because the primary goal of genetic intervention was to eliminate maladaptive morphological traits in the Florida panther (Land *et al.*, 2004), population growth alone is an inappropriate metric for judging the success of this program. A scientifically defensible evaluation of the most recent genetic intervention must include a combination of demography, habitat quality, behavioral ecology and social structure to account for the current distribution of hybrid and purebred panthers in the modern south Florida landscape. Whereas the panther may be better prepared to deal with future landscape and climatic change based on a fortified genotype, the behavioral and demographic responses thus far cannot claim a genetic origin. We offer the following suggestions to better understand the effects of genetic intervention in the Florida panther:

(1) Examine kitten survival and adult reproductive rates in the context of geography and pedigree. That is, control for the influence of panther density and pre-existing social structure in reproductive success and apparent rates of increase. Consider radio-collaring kittens to facilitate the direct measurement of subadult mortality.

(2) Identify and use genetic markers to track the introduced genes of non-Florida cats in the population in relation to the life histories of individuals.

(3) Link habitat use and habitat preferences when discussing spatial aspects of panther distribution and survival. The portrayal of one dot and a line is insufficient to communicate the complexity of Florida panther spatial patterns.

(4) Take into account the hybrid ancestry of the former Everglades population and its demise in the very habitat that a few Texas hybrids are now occupying.

(5) Conduct monitoring over sufficient time that major variation in habitat quality is experienced by Everglades panthers. Only then will insight into the differential survival and reproduction of hybrid panthers be gained.

Now is not the time to celebrate an outcome that has been hoped for by many, but to design and implement rigorous research that evaluates the impact of this genetic management program. Such findings will inform decisions about future management of the Florida panther without relying on whatever data can be strung together from multiple sources.

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frequently. They do not. If enough males are around (even Garp's father was up to the task), population growth depends entirely on the numbers of females. Hybrid females survive better. As most young males disperse, it follows that the successful males who remain will father litters with several females. Our supplemental table (Pimm *et al.*, 2006) shows that they do.

We have a final point of clarification now that Land *et al.*'s (2005) report is available. The supplemental materials reflect the updated information. There are some changes to the known parentage of adult cats and kittens. Of 172 kittens marked by mid-2004 (the end of the period of our analysis), but old enough to receive collars by mid-2005 (the end of reporting by the 2005 report), we now know that 84 kittens have a Texas mother, or hybrid mother or hybrid father. The remaining 88 are purebred or (in some cases) uncertain. (Misclassification of the later would blur the differences between the two groups and make it less likely to be detectable, of course.) Of the kittens, 22 hybrid kittens survived to get collars compared with 11 of the rest. The difference is significant at the $P = 0.01$ level, with a better than a twofold advantage to the hybrid kittens.

Finally, as a matter of disclosure, we have no competing financial interests. Given the controversy our results will create, we urge others to state whether they do or not.

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Ockham and Garp. Reply to Maehr *et al.*'s (2006) response to Pimm *et al.* (2006)

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We find Maehr *et al.*'s (2006) exhaustive recap of his previous controversial positions neither more illuminating nor more plausible than before. (For opinions about Maehr's controversial views on kitten survival and other issues, see Beier *et al.*, 2003, 2006; Gross, 2005; Conroy *et al.*, 2006) From the 'c-statistic' they claim we have used (but we cannot find in our paper) to the impressionistic sketches of panther distributions (devoid of an explicit data source and the methodological details), which purport to replace our maps (that provide both source and methods), we see only obfuscation. Our response recalls William of Ockham's admonition: One should not proliferate hypotheses beyond necessity.

Our hypothesis is simple. After losing habitat, the Florida panther declined to low numbers and its range shrank further. A concomitant increase in observable traits such as kinked tails and cowlicks, as well as other, clearly harmful reproductive ones, were consequences of inbreeding. Genes from Texas cats reversed these trends. Before this genetic rescue, four-fifths of the kittens had kinked tails and cowlicks. Since 2000, only one-third have (Land *et al.*, 2005). The hybrid cats reclaimed areas from where they had previously been lost, including Everglades National Park and the eastern portion of Big Cypress National Preserve. We show the mechanism to be a better than two to one survival of kittens known to have Texas genes over those that do not and the better survival of hybrid females.

Maehr *et al.* promulgate complex, independently unsupported, hypotheses. The first is that the traits we discuss are unrelated to inbreeding (or else inbreeding somehow does not affect fitness), a conclusion substantially at odds with the literature.

Second, they hypothesize that 'if purebred Florida panthers had been introduced in 1995', we might have seen the same result. Their explanations are 'regional differences in habitat quality' and the effects of 'social structure . . . on offspring.' The former requires not only spatial differences in habitat but also temporal ones. They hypothesize that Everglades National Park, having lost panthers in July 1991, inexplicably improved in habitat quality at just the moment hybrid panthers were introduced.

The latter explanation accepts that 'hybrids had some difficulty penetrating areas . . . occupied by resident(s).' We are left confused by Maehr *et al.* conceding they have indeed done well despite that – which is what Maehr *et al.* initially wish to contest. Their solution is the further hypothesis that, having succeeded, the panthers must now fail.

They further assert that 'all known living in the Everglades (before) . . . 1995 were hybrids', – but by South American cats. This altogether remarkable idea is sadly supported by just one 15-year-old reference from a now-extinct journal that used to publish research reports. Fergus (1996, pp. 117–124) provides a detailed discussion of the release of at least seven captive cats between 1957 and 1965 by an owner of a small zoo, Lester Piper. Fergus writes that geneticist M. E. Roelke thought that one of the captive cats was phenotypically from South America. Although the genetic studies apparently confirmed this preconception, Lester Piper denied that any of his cats came from beyond two Florida counties.

The cherry-picked analogy to the tahr is also far-fetched. The vast majority of introductions and reintroductions of species fail, begging the question of what makes any success – and this success – special. 'Coincidentally and against considerable odds' our critics assert; 'measurably better genes,' we reply.

Like Shakespeare's 'second best bed,' our second best model – comparing female survival – is our favorite. It is hardly a 'misleading scenario' for those who understand basic population dynamics or for those who recall Garp's conception by a bed-ridden, comatose, father (Irving, 1982). Only tabloids consider it news when young males disperse and find trouble and then only if they are famous. That young male panthers do the same would matter only if there was a shortage of them for the females that remain. Were males to be in short supply, females would have litters later and less

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