

Evaluating Scientific Inferences about the Florida Panther

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Abstract

At the request of the U.S. Fish and Wildlife Service (USFWS) and the Florida Fish and Wildlife Conservation Commission (FWC), we provide an independent assessment of the reliability of the scientific literature used to support conservation of Florida panthers (*Puma concolor coryi*). We independently reached similar conclusions about unreliable scientific inferences before discussing the issues with each other or with others. Although a quarter-century of research supports many published conclusions, 2 sets of unreliable inferences may compromise efforts to conserve the species. The first is a set of 4 unreliable inferences that underlie the Panther Habitat Evaluation Model (PHEM), used by agencies to evaluate projects that may affect panther habitat. Specifically, the following assertions are unreliable: 1) panthers are forest obligates, 2) panthers require large (>500 ha) forest patches, 3) panthers are reluctant to cross 90-m gaps of nonforest habitat, and 4) the value of potential panther habitat declines linearly with distance to a population core in south Florida, USA. These assertions are unreliable because the analyses excluded (without mention or rationale) almost half the available data, compared used habitats to an inappropriate set of available habitats, made inferences about habitat preference without any data on available habitats, were based only on panther locations during daytime, ignored telemetry error, or suffered from other flaws. The second is a set of 2 unreliable inferences about panther demography prior to the genetic restoration effort initiated in 1995. Inferences that neonate survival was ≥ 0.84 and that the panther population was demographically vigorous prior to 1995 are flawed because the survival analysis ignored mortality during the first 4 months and because other inferences were based on numbers of births and deaths in samples of convenience rather than appropriate vital rates. These faulty inferences about panther demography brought unwarranted credibility to challenges of the genetic restoration program. Faulty inferences of both sets were repeated in subsequent scientific and popular articles; in several instances, previously published work was mis-cited. In its current (2002–2005) version, PHEM is unreliable and should not be used in decisions about panther habitat. Biologists should obtain better demographic estimates and fully analyze how the introgression program has affected these rates. (JOURNAL OF WILDLIFE MANAGEMENT 70(1):236–245; 2006)

Key words

demography, endangered species, Florida panther, genetic restoration, habitat use, *Puma concolor coryi*, reliability, scientific inference.

In 1967, the Florida panther became one of the original entities listed as endangered under the precursor to the 1973 Endangered Species Act. Although *P. concolor* is widespread in South America, Central America, and western North America (where it is called puma, cougar, or mountain lion), in 1967 many experts believed the Florida panther was extinct. Wild panthers were documented in south Florida in the early 1970s (Pritchard 1976), and the first recovery team was appointed in 1976. The 1978 recovery plan was revised in 1987, 1995, and 1999, and it is being revised again in 2005. Management actions to recover the panther have included many science-based actions. For example, state and federal management agencies acquired thousands of acres of panther habitat, captured panthers for a captive-breeding program (but did not breed them), conducted temporary experimental releases of non-*coryi* pumas in a potential reintroduction site in north Florida, implemented a program of genetic augmentation (release of 8 female Texas pumas into the Florida population) in 1995, and conducted several population viability analyses. Radiotracking and biomedical studies of panthers initiated in 1981 have continued without interruption. Approximately 4,000 pages of scientific literature have been published on the panther since 1975, including about 700 pages in peer-reviewed journal articles, 2,050 pages in

agency reports and policy documents, 850 pages in transactions or proceedings, and 350 pages in books and book chapters.

By 2001, scientific controversy about some of these inferences and actions had become so entrenched and personalized that the USFWS and FWC requested an independent review of scientific literature. The agencies feared that without such review the new recovery team might reach an impasse on important scientific issues. Worse yet, the recovery team might reach scientific agreement less on the basis of scientific reliability than on strength of personality, or on the basis of attacks on the competence and integrity of some of the scientists. Under contracts from FWC (Beier and Quigley) and USFWS (Vaughan and Conroy), we formed a Scientific Review Team that evaluated all available published and unpublished scientific literature on the Florida panther, resulting in a lengthy report and annotated bibliography (Beier et al. 2003a). These contracts requested an unbiased review to 1) identify strengths and weaknesses of existing panther data and previously conducted analyses, and 2) identify incorrect or incomplete analyses and interpretation of such data.

In our review, we did not demand incontrovertible proofs of hypotheses. Recognizing that managers need to act on the best available information, we instead evaluated whether the preponderance of evidence supported particular hypotheses, or we evaluated which of several competing hypotheses was best supported by the evidence. In statistical analyses, we evaluated

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the strength of inference in terms of the appropriateness of data inclusion or exclusion, the adequacy of comparison groups, and the appropriateness and interpretation of the analysis. The overriding questions were, “Is the information reliable?” and “Should those responsible for recovery of the Florida panther use this information to make critical decisions that may affect Florida panther persistence?” We operationally defined reliable as the capability of the data, analyses, models, or assumptions to support inferences about the Florida panther and its population dynamics, biology, and habitat use—particularly those inferences used, in turn, to support conservation decisions. We emphasize that unreliable inferences are not necessarily wrong and that future research may support some of these conclusions.

In this paper, we summarize the most important findings of that review. Our objectives are to describe 2 sets of inferences about panther ecology that are unreliable and should not be used to support conservation decisions and to illustrate how selective use of data and flawed analyses can lead to unreliable inference. Many inferences about ecology and management of the Florida panther are sound (Beier et al. 2003a). However, we focus on unreliable inferences; this creates a regrettably negative tone to the text. We hope that our explanations of why these inferences are unreliable and how poor inferences can affect management will form the basis for better management of endangered species and other wildlife.

Deconstructing science is grim work, and we realize how each of us would feel if our scientific labors suffered a fate similar to some of the inferences described herein. Reluctant to publicize our blunt criticisms, we waited a full year after acceptance of our report to begin work on this paper. We focus our criticisms on scientific inferences, not on the scientists involved. We believe that questioning the integrity of scientists is counterproductive. In particular, several of us have worked with David Maehr in various contexts; we respect his intellect, and we hope that we will continue to collaborate with him, productively and respectfully, in the future. There is much work to be done in wildlife management and conservation biology—we need to build up, not tear down, all the good minds available for this work.

Methods

When we began our work as a Scientific Review Team, none of us had prior knowledge of scientific controversies related to panther management. At our initial meeting in late April 2002, we asked FWC and USFWS if we should be aware of any particular disputes. The agency representatives responded that controversies existed, but they admonished us to let the literature speak for itself and to insulate ourselves from any other inputs. We thus decided not to discuss issues with anyone (not even each other) until we each had independently evaluated the literature.

In May 2002, we classified the approximately 4,000 pages of published and unpublished papers into topical areas and assigned ourselves (in subteams of 2 persons) to review the literature in each subject area. About 20% of the papers straddled topical areas and were assigned to 2 or more subteams. By September 2002, each of us had evaluated material in our assigned topical areas. At this time, each pair of reviewers provided a list of 8–11 key papers from each topical area for review by all members of the Scientific Review Team, without advice on why the paper had been selected.

Thus, each paper was read by at least 2 members of the Scientific Review Team, and all members read the most important papers. During this phase, Scientific Review Team members carefully avoided commenting to each other about the readings. When interested parties contacted us during this phase we refused to discuss our review or listen to their comments; when comments were sent to us, we set the comments aside without reading them until after we met in November 2002. Thus, each reviewer independently evaluated the literature on its merits.

During 4–7 November 2002, we met again and, for the first time, discussed our evaluations of the literature. Each Scientific Review Team member approached that meeting with strong reactions to certain portions of the literature, and with some degree of apprehension that his reactions might not be shared by the rest of the team. However, in each subject area, we unanimously agreed about the strengths and weaknesses of the data and analyses. After our initial discussions and agreement on the major areas of unreliable inference, we ended our self-imposed isolation. Subsequent communication with various persons clarified areas of ambiguity but did not substantially alter our initial, independent evaluations. These communications included e-mails, telephone conversations, and personal interviews with Oron L. Bass, R. Christopher Belden, E. Jane Comiskey, Mark W. Cunningham, Deborah Jansen, John W. Kasbohm, E. Darrell Land, David S. Maehr, Roy McBride, and others. In the few instances that private lobbying was directed at one of us, each of us immediately forwarded the e-mail or e-mailed a summary of the relevant telephone conversation to the other members of the Scientific Review Team.

We submitted our draft review to USFWS and FWC in June 2003. The agencies distributed this draft to 6 anonymous reviewers they recruited, and they provided copies of the draft to members of the recovery team and to the Panther Subteam of the Multi-species/Ecosystem Recovery Implementation Team (MERIT) who were invited to submit comments directly to the Scientific Review Team. The 6 solicited reviews were returned to the agencies, which in turn provided the reviews to the Scientific Review Team on 9 September 2003, maintaining reviewer anonymity. Our final report (Beier et al. 2003a), including an annotated bibliography of the literature we reviewed, was accepted by the agencies in December 2003. A second document (Beier et al. 2003b) contains all written communications received by the team, including 45 pages of comments in addition to the formal reviews.

One year after acceptance of our final report, we distilled from our report this pointed evaluation of 2 sets of inferences. The first set includes 4 inferences about habitat use by panthers; these 4 inferences in turn lie at the core of a model used to evaluate and mitigate potential impacts to panther habitat. The second set includes 2 inferences about panther demography that in turn were used to question the need for the 1995 introgression program and to parameterize models of panther population viability. We chose these 2 examples because they have important implications for management of panther habitat and how managers and citizens perceive the genetic restoration program and because they provide the background for a companion paper (Conroy et al. 2006) that discusses scientific method, the peer-review process, and the role of science in endangered species management.

Table 1. The 6 factors of the Panther Habitat Evaluation Model (Maehr and Deason 2002), scientific inferences used to support each factor, and scientific issues that could render these inferences unreliable.

Factor (weight): scoring	Underlying scientific inference and source(s)	Scientific issues
1. Vegetation type (25%): maximum for hardwood hammock; 20% for cypress, hardwood swamp, pineland; 15% for thicket swamp, scrub; 10% for farms; 5% marsh, barrens; 0% developed, open water.	Panthers are forest obligates (Maehr 1997a, Maehr et al. 2001) Panthers prefer forest habitat (Maehr and Cox 1995)	Maehr et al. (2001) and Maehr (1997a) offered rhetorical arguments for importance of forest but ultimately relied on Maehr and Cox (1995) for support. The analysis excluded ~40% of panthers using less-forested landscapes. Available habitat included some land outside panther range and some less-forested habitat used by panthers excluded from the analysis. Inference based on locations obtained during daytime; this fact was not mentioned by Maehr and Cox (1995). Chi-square and other analyses treated the location rather than the animal as the sampling unit; such analyses are pseudoreplicated.
2. Size of forest patch (25%): maximum for patches >600 ha, 20% for 400–600 ha, 10% for 200–400 ha, 0% for 200 ha	“A linear regression of patch size showed that panther occupancy became more likely in patch sizes greater than 500 ha” (Maehr and Cox 1995). “Only 25% of the panther locations occurred in [forest] patches smaller than 500 ha” (Maehr and Cox 1995).	The quadrat-size effect guarantees that panthers are more likely to occur in larger patches. An analysis using per-ha likelihood of occurrence is required to determine whether panthers prefer large forest patches. Because these results were not compared to the size distribution of forest patches available to panthers, these data do not support any inference about panther preference or avoidance of large forest patches.
3. No discontinuities in forest cover 90 m wide (5%): 0% if discontinuity >90 m	Maehr et al. (2001) and Maehr and Deason (2002) asserted panthers were reluctant to travel across unforested habitat 90-m wide and attributed this inference to (Maehr and Cox 1995).	Maehr and Cox (1995) made no such claim but did report 96% of all panther locations occurred within 90 m of forest cover. Almost all locations were obtained during 0700–1200, when panthers are typically bedded for the day; such locations do not support inference about habitats traveled by panthers at night. Analysis assumed zero m location error and no error in GIS vegetation polygons. Using the same procedures to collect some of these same data, Belden et al. (1988) estimated location error as 230 m.
4. Proximity to the “panther population core as defined by Maehr (1997a)” (20%): score maximum in the core, declining linearly to 0% at 50 km.	Maehr (1997a:210–215) presented a map of this area and rhetorical arguments for its importance, explained its boundaries as that of a “continuous green blob” in a satellite image, and referred to Maehr and Cox) as the primary support.	The inference is circular: Maehr and Cox (1995) compared the area used by 23 forest-dwelling panthers to a larger area with less forest cover; the resulting model predicted that the forested area occupied by these 23 panthers is the best habitat; Maehr (1997a) then used Maehr and Cox (1995) to defend this study area as a “panther core” representing the best panther habitat. No rationale for habitat value declining linearly with distance from the core to zero at 50 km.
5. Contributes to connectivity of panther habitat (15%): 15% if loss of land would fragment panther habitat.	Panthers live at low density, have large home ranges, and suffer from frustrated dispersal (Maehr et al. 2002b).	No scientific issues; inferences appear reliable. However, depending on how the scoring is implemented, the forest-centered definition of panther habitat could bias the calculation.
6. Degree to which land is surrounded by potential panther habitat (10%): 2.5% for each cardinal direction with suitable habitat.	Same as previous. In addition, there is increased potential for conflict with humans at interface with human-dominated landscapes.	No scientific issues; inferences appear reliable. However, depending on how the scoring is implemented, the forest-centered definition of panther habitat could bias the calculation.

Results

Inferences Underlying the Panther Habitat Evaluation Model

The Panther Habitat Evaluation Model (Maehr and Deason 2002) affects important decisions on land use and consultations under the Endangered Species Act. The goal of PHEM is to provide “an empirical approach [that] can be used by permitting

agencies to ensure an objective and consistent landscape approach to panther conservation throughout south Florida. . . It is intended for use on lands that are proposed for development as well as for property that [may be acquired to conserve panther habitat]” (Maehr and Deason 2002:398). The PHEM produces “an estimate of functional equivalent units of panther habitat” (Maehr and Deason 2002:398) based on weighted scores for 6 habitat factors (Table 1). The first 4 factors (comprising 75% of the

weighting in the PHEM) hinge directly on 4 inferences; Maehr and Deason (2002) attribute the first 3 factors to a single paper by Maehr and Cox (1995) and the fourth to Maehr (1997a). We describe each of these inferences in relation to the relevant factors in the PHEM (Table 1).

Inferences about the importance of forests to panthers.—Maehr and Deason (2002) cited Maehr et al. (1991b), Maehr and Cox (1995), and Maehr (1997a) to support this weighting. Maehr et al. (2001:293) stated, “Unlike conspecifics in western North America, the panther is an obligate forest creature,” and cited an earlier monograph (Maehr 1997a) as authority for this idea. Although Maehr (1997a) apparently did not use the term “forest obligate,” the book did champion the importance of forests to panthers in vivid terms, such as, “Panthers living in [areas with little forest cover] are essentially the ‘living dead’ of the population” (Maehr 1997a:213). The book provided anecdotal arguments for the importance of forests, but it based its conclusions about the importance of forest primarily on a single, peer-reviewed paper that included original analysis of field data (Maehr and Cox 1995). Similarly, assertions about the importance of forest habitat by Maehr and Deason (2002) and Maehr and Meegan (2001) were referenced to the Maehr and Cox (1995) paper, to an earlier paper using a subset of the same data published in *National Geographic Research and Exploration* (Maehr et al. 1991b), or to other papers that in turn refer to these papers as the authority for the relevant assertions. Thus, all inferences about the importance of forests to panthers ultimately point to Maehr and Cox (1995).

Maehr and Cox (1995) analyzed thousands of panther radio locations and concluded that forests were the most important vegetation type for panthers. Approximately 14,500 radio locations from 41 panthers were available for analysis by Maehr and Cox (1995), who claimed to use “14,548” panther radio locations (their Abstract, p. 1008) and “14,509 radio-telemetry points” (their Methods, p. 1010). The paper included a map captioned “South Florida study area” (Fig. 1A in our paper) that encompassed the range of all 41 radiotagged panthers (Fig. 1B). This, together with a second map predicting potential panther habitat within the same geographic area, led each of us to assume that all animals in that landscape were included in their analyses. The authors compared these radio locations to 8,500 “random” locations, a number justified because it, “approximated the average of 382 locations for each of 23 panthers” (p. 1010). After we learned that 41 (not 23) panthers had been available for analysis, we sent inquiries to the authors asking which animals and locations were used. From the senior author’s response, we learned that the analysis included data from only 23 animals, totaling about 8,600 locations, and the analysis was restricted to a small portion of the south Florida study area (Fig. 1C). Thus, Maehr and Cox (1995) excluded >40% of the available panthers and radio locations from their analyses.

To quantify habitat selection, Maehr and Cox (1995:1010) compared these panther locations to a set of random locations, namely, “randomly generated locations within 40 km of a known panther location [which is] approximately twice the maximum distance traveled by a panther in 24 hours.” This 40-km buffer (Fig. 1C) probably included areas outside the range of the panther,

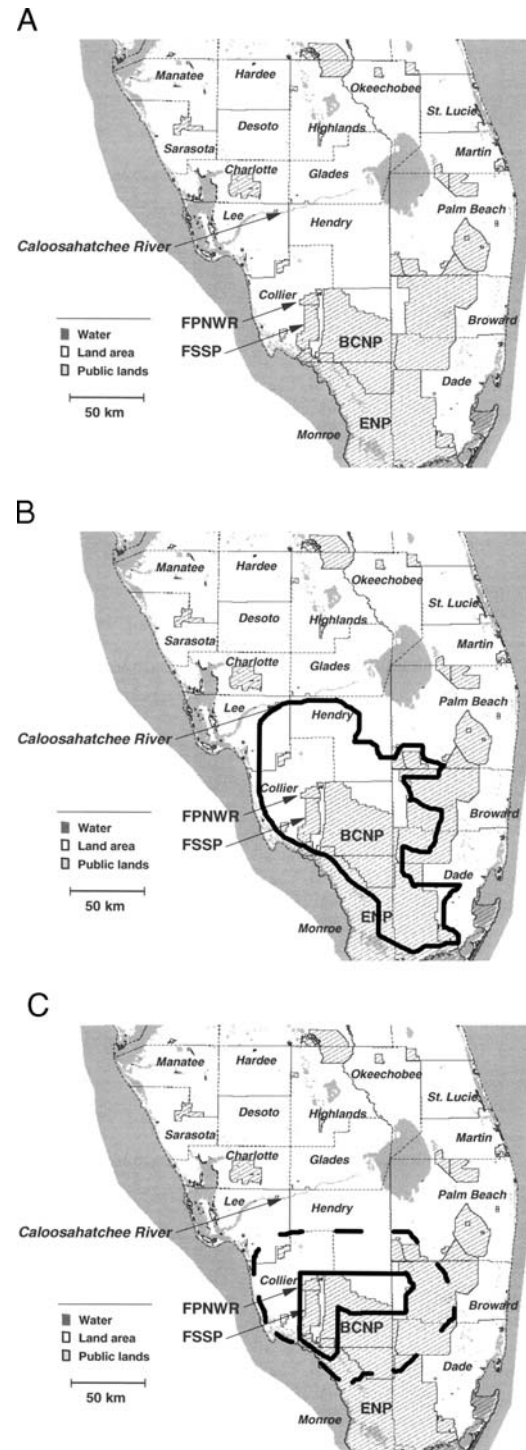


Figure 1. (A) Figure 1 from Maehr and Cox (1995), where the original caption was “South Florida study area showing major public lands and county borders.” (B) The same base map as Figure 1A with additional polygon that encompasses approximately 14,500 radio-locations of the 41 panthers for which data were available at that time. (C) The smaller polygon encloses approximately 8,600 radio-locations of 23 panthers included in the analyses of Maehr and Cox (1995). Maehr (1997a) and Maehr and Deason (2002) later referred to this area as the “panther population core.” The larger dashed polygon extends 40 km from the smaller polygon and is thus the area within which random locations were generated for comparison to the 8,600 panther locations. This larger area includes some areas used by the 18 panthers excluded from the analysis, as well as some areas outside known panther range. The facts and relationships conveyed in Panels B and C were not conveyed in the text or supporting elements of Maehr and Cox (1995). Figure reproduced with permission of Blackwell Publishing Ltd.

including urban land, water impoundments, and large expanses of row crops. Some of the areas in this 40-km buffer were used by the 18 panthers excluded from the analysis (Fig. 1B). Because the area used by the 23 panthers in the analysis included some of the most heavily forested parts of south Florida occupied by radiotagged panthers (maps in Florida Panther Subteam of MERIT 2002), the analysis compared habitats used by panthers in a heavily forested study area to a much larger “available area” that, on average, had less forest cover.

Inference that panthers need forest patches >500 ha.—Maehr and Deason (2002) cited Maehr and Cox (1995) as the authority for this idea. The abstract of Maehr and Cox (1995:1008) stated that, “patches larger than 500 ha are important for panther occupation.” This conclusion is based solely on 2 analyses (not mentioned in the methods section) described in the following 2 sentences in the combined results and discussion section: “A linear regression of patch size showed that panther occupancy became more likely in patch sizes greater than 500 ha, and only 25% of the panther locations occurred in patches smaller than 500 ha. These results suggest that patches of this general size may be needed for frequent panther occupation” (p. 1014–1015).

The first analysis, a regression, indicated a positive relationship between panther occupancy and patch size. Although Maehr and Cox (1995) did not define “panther occupancy,” only 2 definitions seem possible: 1) the number of panther locations in a patch of a given size, or 2) percent of patches of a given size that contained at least 1 panther location. In either case, large quadrats (sampling areas) inevitably contain more of whatever is being tallied; this will guarantee a positive slope in such a regression.

The second analysis relied on a frequency distribution of patch sizes used by panthers. This distribution was not compared to a frequency distribution of patch sizes available to panthers. The authors did not report the availability of patch sizes, nor did their analysis indicate any comparison to patch sizes available to panthers.

Inference that panthers are reluctant to cross 90-m gaps of nonforest habitat.—Maehr et al. (2001:298) stated that, “Panthers seem reluctant to travel across unforested habitat that is greater than 90 m in width... (Maehr and Cox 1995).” Maehr and Deason (2002:401) repeated this claim and again cited Maehr and Cox (1995) as their authority. In fact, Maehr and Cox (1995) made no such claim. The closest relevant statement in their paper was that, “96% of all panther locations occurred within 90 m of preferred land cover” (p. 1008, 1018). This “90 m” distance is accurate only if telemetry location error was 0 m. Over 99.6% of the panther locations analyzed by the authors were obtained during daylight hours, of which >85% were obtained during 0700–1200 (Maehr et al. 2004).

Inference about the value of proximity to a population core.—Twenty percent of the PHEM score accrues to how close a particular parcel is to “the Florida panther population core as defined by Maehr (1997a)” (Maehr and Deason 2002:401). Thus Maehr’s (1997a) book is the sole authority for the boundaries of the core area and its importance to panthers. Although Maehr and Deason (2002) did not reference specific page numbers, pages 210–215 of the book present a map of the core area and rhetorical arguments for its importance. The population core mapped by

Maehr (1997a: his fig. 14.2) was apparently the area used by the 23 panthers included in the analyses by Maehr and Cox (1995; i.e., the small polygon in Fig. 1C).

Maehr (1997a) argued that the population core had a high and stable density of panthers, but it did not provide quantitative support for these assertions. In the text introducing his fig. 14.2, Maehr (1997a:211–212) defines the core area as a “continuous green blob” that stands out on a satellite image of south Florida. No more rigorous definition of its boundaries was offered. Maehr and Deason (2002) did not present a map of the population core, nor did they present any description of its location. Neither Maehr (1997a) nor Maehr and Deason (2002) offered any reason why habitat value would decrease linearly with distance from this population core, nor why the proximity score reaches zero at a distance of 50 km.

Inferences about Florida Panther Demography

Maehr and Caddick (1995) inferred that, prior to genetic restoration in 1995, the panther population was demographically vigorous and tracked carrying capacity, and kitten survival rates exceeded 80%. These inferences were subsequently used to parameterize a Population Viability Analysis (PVA) for panthers (Maehr et al. 2002a), and to support other arguments (Maehr 1997a,b, 1998, Maehr and Caddick 1995, Maehr et al. 2001, Maehr and Lacy 2002). Unlike a usual refereed paper, Maehr and Caddick (1995) was a 3-page note that lacked a *Methods* or *Results* section.

Inference that the pre-1995 panther population was demographically vigorous.—Maehr and Caddick (1995) presented a plot of the numbers of kittens born to tagged animals against the number of deaths of radiotagged animals (all tagged as adults) in each of several years (Fig. 2), and they interpreted this figure as indicating a “positive growth rate” (p. 1297). These births and deaths did not have a common population base because none of the kittens were radiotagged and therefore could not contribute to the tally of mortalities. The graph depicted raw numbers of detected births and detected deaths, and the authors did not express the results as birth and death rates.

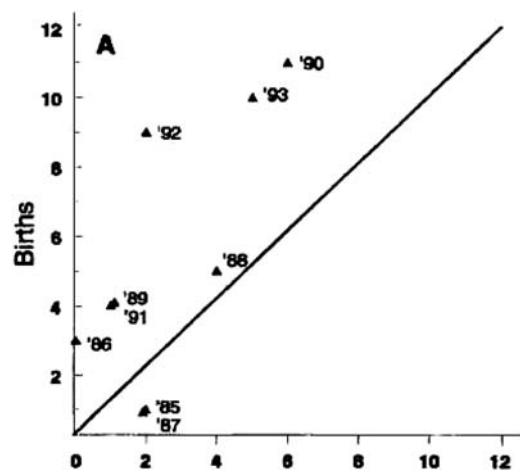


Figure 2. Numbers of kittens produced by year in relation to deaths of radiotagged animals, originally produced in fig. 1 in Maehr and Caddick (1995), where the caption read “Known births versus known radiocollared panther deaths... from 1985–1993.” Figure reproduced with permission of Blackwell Publishing Ltd.

Estimates of kitten survival rate.—Without providing tables or other descriptions of the data or methods, Maehr and Caddick (1995:1295) estimated kitten survival rate at 84 and 87% in the following 4 sentences:

Known kitten production from 1985 through 1993 revealed a mean litter size of 1.92 ($n=25$ litters, range 1–4). Four neonate litters 14 days old or younger averaged 2.25 (range 1–3), and litters from 4 to 12 months of age averaged 1.89 (range 1–4). The differential between neonates and older kittens suggests a first-year survival rate of 0.84 ($1.89/2.25 = 0.84$). When only radiocollared kittens older than 4 months but less than 12 months are considered, a survival rate of 0.87 is obtained (2 deaths out of 15).

The 84% estimate was not based on litters followed over time but rather on litter sizes at 2 different ages. This will reflect survival rate only if the samples are representative and detectability of kittens is independent of age (Williams et al. 2002:343ff). The cubs in the older kittens' age class actually included litters aged 4 months through 12 months. Thus, this is not an annualized survival rate, nor can an annual rate be reconstructed from these data. The second estimate is similarly not an annual estimate because it covers a period of at most 8 months per kitten, and the annualized rate depends on how many of the 15 kittens were radiotagged in each month.

Discussion

Inferences Underlying the Panther Habitat Evaluation Model

Scientifically rigorous conclusions regarding Florida panther habitat requirements are critical because they affect land management decisions, particularly those made in USFWS Section 7 consultations on land development and mitigation, where the best available science is the standard. It is important to carefully consider what conclusions are supported by the preponderance of evidence and can thus be considered reliable because the Endangered Species Act does not define best available science and because nothing in case law suggests that best available science is synonymous with published, peer-reviewed, or most recent (Bean and Rowland 1997). Unfortunately, we concluded that 4 inferences—constituting 75% of the weighting in PHEM (Maehr and Deason 2002)—are unreliable. These 4 inferences concern the importance of forests to panthers, panther preference for forest patches >500 ha, panther reluctance to cross >90 m of nonforest, and decreasing value of habitat with increasing distance from a putative panther core.

Inferences about the importance of forests to panthers.—Conclusions about the importance of forest vegetation to panthers derive from an analysis by Maehr and Cox (1995) that suffered from 2 serious flaws. First, the authors excluded about 40% of the data available for the relevant analyses. Although every analysis of radio-location data excludes some data, investigators usually explain and justify how data were screened (e.g., Dees et al. 2001). In contrast, the authors failed to mention that they excluded 18 of 41 radiotagged animals and about 6,000 of some 14,500 radio locations available at that time. Even a careful reading of this paper would not suggest that some data were excluded. Second, the authors compared the habitats used by these

23 panthers to an inappropriate set of available locations; this was inappropriate because some of these areas were outside the known geographic range of panthers and other areas were actually used by panthers that were excluded from the analyses.

These 2 flaws acted synergistically to guarantee an analysis biased toward the importance of forests. Because the area used by the 23 panthers in the analysis included some of the most heavily forested areas occupied by panthers, the analysis compared habitats used by panthers in a heavily forested study area to a much larger available area that, on average, had much less forest cover. Thus, the analysis of Maehr and Cox (1995) inevitably reached the conclusion that panthers prefer forests. These analyses also suffered from pseudoreplication and inappropriate extrapolation from daytime locations (Table 1). Although normally considered serious, these latter errors pale beside the structural flaws in the analysis.

We found that inferences about the importance of forests are unreliable. It does not necessarily follow that such conclusions are wrong. Despite all of these problems, future analyses may demonstrate that forests are the most important vegetation type for panthers in south Florida. However, Maehr and Cox (1995) cannot support claims that the panther is a forest obligate, and they cannot provide the basis for the vegetation scores used in the PHEM. In Conroy et al. (2006), we elaborate on this distinction between reliability and truth.

Inference that panthers need forest patches >500 ha.—Maehr and Cox (1995) used 2 defective analyses to support this inference. We believe that if these analyses had been mentioned in the methods section, a reviewer would have noticed their flaws; instead, the 2 analyses were summarized in 4 sentences in a long results and discussion section. The first analysis, a regression, had a positive slope due to the quadrat-size effect. This effect guarantees that a linear regression on patch size would show that occurrence of any entity (a pond, for instance) is more likely in patches >500 ha. The second analysis, a frequency distribution of the sizes of forest patches used by panthers, is uninformative because the authors failed to compare it to the distribution of patch sizes available to panthers. The fact that 75% of panther locations occurred in patches >500 ha would yield different inferences depending on the proportion and distribution of such patches in the home ranges of radiotagged panthers and depending on how fitness of individual panthers varies with home-range composition (Garshelis 2000). Because both analyses provide no inference about panther behavior with respect to patch size, there is no empirical support for the idea that 50 ha within a large forest patch is more valuable to panthers than 50 ha within a smaller forest patch.

Inference that panthers are reluctant to cross 90-m gaps of nonforest habitat.—In this case, the unreliable inference was due only partly to a defective analysis in Maehr and Cox (1995). The more serious scientific failure was the over-interpretation of the 1995 paper by Maehr et al. (2001) and Maehr and Deason (2002), who wrongly attributed the inference to Maehr and Cox (1995).

Maehr and Cox (1995) did state that 96% of panther locations were <90 m from forest cover. This claim should be amended to reflect errors in radio locations and vegetation maps. Even after amendment, however, this result provides no basis for inference

about “reluctance to cross” nonforest habitat because >99.6% of these panther locations were obtained during daylight hours, and mostly during 0700–1000 (Maehr et al. 2004). Daytime locations do not reflect how panthers behave at night when most puma travel occurs (Beier et al. 1995), and habitat use is broader than that observed during daylight (Dickson et al. 2005). By way of analogy, almost all locations of most humans during 2000–0100 (a 5-hr period after our peak of activity) are in our homes; this does not justify any inference about a general reluctance to leave our houses at other times of day.

Maehr et al. (2004) argue that panthers, unlike other pumas, might be nearly as active during the daytime as at night, and imply that daytime locations might therefore accurately reflect 24-hr habitat use. We find this analysis unpersuasive because it was based on activity at <49 nighttime locations (the exact number is obscured by broad time classes) out of about 14,500 locations and because it estimated activity as indicated by the movement of a motion-sensitive switch in the radiocollar instead of distance moved. The inference that panthers are reluctant to cross nonforested land is further contradicted by the observation (Maehr et al. 1992) that an adult male panther in an area of fragmented habitat (65% of his home range was urban, agriculture, and unforested) regularly crossed large nonforest areas within his home range.

Inference about the value of proximity to a population core.—The population core mapped by Maehr (1997a: his Fig. 14.2) corresponds roughly to the small polygon in our Fig. 1C (i.e., the area used by the 23 panthers included in the analyses by Maehr and Cox [1995]). Maehr (1997a) cited Maehr and Cox (1995) as the main authority for the importance of this core. However, this argument is circular: comparing the area used by these 23 panthers to a larger area with (on average) less forest cover led Maehr and Cox to develop a habitat model; this model predicted—inevitably, given its structure—that the forested area occupied by these 23 panthers is the best habitat; then Maehr (1997a) cited Maehr and Cox (1995) to justify mapping the area used by these 23 panthers as a “panther population core.”

Maehr (1997a) and Maehr et al. (2001) used this inference, along with the assertion that panthers are forest obligates, to denigrate the value to panthers of vast tracts of public land including Everglades National Park and most of Big Cypress National Preserve. Maehr (1997a:213) wrote, “the few panthers living in such marginal range are essentially the ‘living dead’ of the population.” Prior to release of female Texas pumas into Big Cypress and Everglades in 1995, most of the panthers that were most intensely monitored resided in this population core. However, immediately after release of the Texas animals, panthers survived and reproduced in areas that did not meet the PHEM criterion of proximity to a hypothesized panther population core (Shindle et al. 2001).

Building a New Panther Habitat Evaluation Model

Reanalysis of existing data can quickly yield a model superior to the PHEM. Although existing data are restricted to locations obtained during 0700–1200, careful interpretation can avoid pitfalls associated with this limitation of the data. All other flaws (Table 1) can be fully remedied by appropriate analyses. Because all these remedies were available in 1993, scientists and managers

are now dealing with unreliable inferences that could have been avoided. However, at this point the important issue is not to assign blame but to avoid compounding errors by prolonging them. We are pleased that on 26 March 2005, the FWS formally decided to thoroughly revamp their Landscape Conservation Strategy (a December 2002 version of PHEM) by December 2005 in response to our report, and they will also update certain biological opinions that were based on flawed inferences.

Inferences about Florida Panther Demography

Maehr (1997a,b, 1998), Maehr and Caddick (1995), Maehr et al. (2001), and Maehr and Lacy (2002) questioned the need for the genetic restoration program that began in 1995 with the release of 8 Texas pumas into south Florida. These papers relied on inferences by Maehr and Caddick (1995) that, prior to genetic restoration, the panther population was demographically vigorous and tracked carrying capacity, and that kitten survival rates exceeded 80%. This kitten survival estimate was further used in a PVA by Maehr et al. (2002a) that predicted no demographic benefit from genetic introgression.

Unreliable inferences about pre-1995 vigor.—It is important to note that 1 graph and 4 sentences in Maehr and Caddick (1995) constitute all the empirical support for pre-1995 demographic vigor of panthers. All other papers restate and amplify the 2 central claims of Maehr and Caddick (1995), but they offer no new supporting data or analysis.

Maehr and Caddick (1995:1297) inappropriately interpreted their fig. 1 (our Fig. 2) as indicating a “positive growth rate.” These data cannot be reliably used to infer population growth rates, for 2 reasons. First, despite the naïve appearance of a common basis (births to or deaths of 1 set of radiotagged panthers), in fact the kittens were not radiotagged and thus could not contribute to the tally of mortalities. Second, these data are uncorrected for incomplete and likely heterogeneous detection in both types of sample data (Williams et al. 2002). The position of points in such figures (our Fig. 2) largely reflect researchers’ ability to detect births and deaths, and these points cannot be used to infer birth and death rates needed to determine whether population growth is positive or negative. Calculation of growth rate requires per capita vital rates, which are not depicted in figures like these. Such figures invite misinterpretation, and should not be included in scientific publications.

The kitten survival rates in Maehr and Caddick (1995) fail to qualify as annual survival estimates and cannot be considered reliable. The 84% estimate was based on mean litter size at 2 ages, which reflects survival rate only under certain restrictive and unlikely conditions (Williams et al. 2002:343ff). Perhaps more important, the litters in the older-kittens age class actually included litters aged 4 months through 12 months. Thus, 84% is not an annualized survival rate, nor can an annual rate be reconstructed from these data because the actual ages of the older kittens are not given. Although these data suggest that survival rate of neonates did not exceed 84%, the actual rate cannot be calculated.

The 87% kitten survival rate ignores mortality from birth to 4 months; furthermore, survival over the 8-month interval depends on how many of the 15 kittens were tagged in each month. Survival rates can be calculated only on the basis of exposure-days and actual age at the start of monitoring, for each sex-age class

(Williams et al. 2002:343ff). The finding of “2 deaths out of 15” sets an upper limit of 87% on neonate survival, but it does not yield a reliable survival rate. Moreover, this estimate of 84–87% kitten survival was higher than the 82% estimate for Florida panthers of all ages, mostly adults (Maehr et al. 1991a). Although it would be unprecedented in studies of vertebrates for the survival rate of juveniles to equal or exceed adult survival rate, Maehr and Caddick (1995) did not mention or discuss this striking divergence from previous work. Shindle et al. (2001), whose report included raw data used to compute these estimates, estimated that Florida panther kittens unaffected by genetic augmentation had a 52% survival rate during 1995–2000. Thus, the estimate of 84–87% kitten survival is not supported by data and should not be used in population projections.

Finally, it is significant that Maehr and Caddick (1995) lacked a Methods or Results section; we believe the publication is best characterized as an editorial. It was entirely appropriate for a scientist of David Maehr’s stature to write an editorial on the genetic restoration program in 1995. It was equally appropriate that the editorial was published rapidly, while there was still time to halt or modify the experiment. However, it was not appropriate to offer scientific inferences within an editorial or to later cite that paper as if it had been a rigorously peer-reviewed paper (see Conroy et al. 2006).

Uncritical Use of Unsupported Kitten Survival Rates.—Maehr et al. (2002a) used kitten survival estimates from Maehr and Caddick (1995) in a PVA that estimated extinction risk at 0%, in contrast to a 100% extinction risk estimated by previous PVAs (Seal and Lacy 1989, Seal 1992). Sensitivity analysis conducted by Maehr et al. (2002a) suggested that neither habitat trend nor continued genetic augmentation, nor interactions between them, influenced their estimates of extinction risk. However, Maehr et al. (2002a) did not conduct sensitivity analysis for the 3 largest changes in their model parameters compared to previous panther PVA, namely increasing kitten survival from 0.50 to 0.80, increasing carrying capacity from 50 to 70 breeders, and increasing initial population size from 50 to 60 breeders.

Understanding the sensitivity of PVA to these parameter changes is more important than the point estimate of extinction risk. Ellis et al. (1999:65) analyzed sensitivity of PVA (with the same structure as the PVA used by Maehr et al. 2002a) to kitten survival rate over the range of 40% to 80%. These results suggest that kitten survival <60% led to negative growth rates and rapid extinction. Ellis et al. (1999) concluded that this sensitivity justified greater research effort to estimate kitten survival rates. In contrast, Maehr et al. (2002a) used the estimate of 80% kitten survival rate, praised it as based on “2 decades of . . . long-term demographic research that minimizes speculation” (p. 286) and did not conduct sensitivity analysis on this parameter.

Understanding the Effect of Genetic Introgression on Panther Demography

We believe that unreliable inferences about panther demography muddled the debate about the viability of the panther population and thus brought unwarranted credibility to arguments that genetic restoration might not benefit panthers. As noted above, however, the fact that these inferences are unreliable does not

necessarily mean they are wrong. We urge management agencies to collect and promptly analyze data to determine the impact of genetic management on vital rates. By 2003, it was already impossible to know the pedigree of many panthers, so recent data provide a unique opportunity to compare purebred Florida panthers with hybrids in analyses unconfounded by the effects of time and location. Such analyses promise to make the Florida panther the textbook example of the relevance of genetics to conservation; this study will be far more compelling than any previous study (Beier et al. 2003a:33–34).

We reject the idea that, because genetic introgression is a fait accompli, there is no point in these analyses. For decades, many scientists have doubted whether genetics is relevant to in situ conservation (Landé 1988, Caro and Laurenson 1994, Caughley 1994, Nash 2001). The first poster child for the role of genetics, the cheetah, has lost some of its credibility (Laurenson et al. 1995). A recent analysis of butterfly extinction (Saccheri et al. 1998) showed that genetics, while important, were less important to extinction than other factors, and the lessons of Saccheri’s study are arguably of limited relevance to the species and landscapes typically managed for conservation. The story of decline and recovery of prairie chickens (Westemeier et al. 1998) is more persuasive and does incorporate measures of pre-bottleneck diversity (Bouzat et al. 1998), but it is based on comparisons of populations before and after introgression without measuring the genetic variability or the demographic performance of inbred and outbred individuals or without controlling for effects of place and time. The Florida panther story may become the best documented example of the relevance of genetics to conservation.

Management Implications

Because at least 75% of the PHEM score is based on unreliable inferences (Table 1), we recommend that PHEM not be used as the basis for decisions about managing Florida panther habitat. Fortunately, reanalysis of existing data can quickly yield a superior model, as described above, and USFWS is taking decisive steps in this direction.

We believe that genetic outcrossing has enhanced demographic performance of the panther population and that the paper by Maehr and Caddick (1995) injected unreliable inferences into this discussion. Because future conservation decisions deserve to be informed by the results of the panther introgression experiment, we urge agencies and scientists to seize the opportunity to rigorously address this issue.

This review caused us to reflect about the nature of scientific inquiry and publishing. In keeping with our philosophy that the scientific literature should segregate editorializing from papers presenting scientific inferences, in a companion paper (Conroy et al. 2006) we suggest changes to the process of peer review and urge applied ecologists to view science as an adaptive process that works best when practitioners have multiple working hypotheses.

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service of science and conservation. They are true panther experts—we have become experts only to the extent that we have peeked over their shoulders. Their status as experts cannot be taken away by criticism, nor is our criticism intended to do so. The fact that panthers are better off now than they were 20 years ago is to their credit. Most research has been of high quality, a fact that tends to get lost in a paper like this.

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