

Endangered Florida panther population size determined from public reports of motor vehicle collision mortalities

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Summary

1. Reliably estimating the abundance of rare or elusive animals is notoriously difficult. An archetypical example is the endangered Florida panther, whose conservation status is intrinsically linked to population size, but for which reliable abundance information is lacking across its range. This is due not only to the inherent difficulty of sampling a rare and elusive species over a large geographic area, but also because of restricted scientific access to private land.

2. Human interactions with wildlife are a regular occurrence, and interactions with non-scientists constitute an important and underutilized source of information about species distribution and abundance. For example, motor vehicle collisions with Florida panthers are recurrent on the vast network of roads within the public and private lands comprising its range in southern Florida, USA.

3. Capitalizing on a tendency for the public to report collisions with species of concern to wildlife officials, we describe a novel methodology using public reports along with routine telemetry monitoring data to produce the first statistically defensible population estimates for the Florida panther across its entire breeding range. In essence, our approach uses traffic volume and road density to estimate the probability of motor vehicle collision mortality from telemetered animals and models counts reported by the public accordingly.

4. Despite low motor vehicle collision mortality probabilities, our methodology achieved abundance estimates of reasonable precision (29% CV) that was similar to that of previous panther studies using conventional approaches on much smaller study areas. While recovery criteria require establishment of three distinct populations of 240 Florida panthers, we found this single population may never have exceeded 150 individuals from 2000 to 2012.

5. *Synthesis and applications.* By extracting critical demographic information from underutilized aspects of human–wildlife ecology, our citizen-based approach can cost less than conventional alternatives and could conceivably be used for long-term population monitoring of other species over broad geographic areas, for example from reports of avian wind farm collisions, beached whales or marine mammal boat strikes. An additional benefit is that it can be applied to historical data sets of carcass recovery programmes, in our case permitting abundance estimation over a 13-year period.

Key-words: abundance, capture–recapture, citizen science, dead recovery, human–wildlife ecology, imperfect detection, mark–resight, *Puma concolor coryi*, risk of collision, telemetry

Introduction

The estimation of population size for wild animals is essential to responsible management and testing ecological or evolutionary theory. Over the past four decades, a

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large variety of statistical methods have been developed for estimating the abundance of diverse taxa when detection probabilities are <1 , including capture–recapture and distance sampling methods (e.g. Williams, Nichols & Conroy 2002). Invariably, there are cases where these now-traditional methods are challenged by ethological (e.g. reclusive or elusive behaviour), demographic (e.g. rare or low density), geographic (e.g. remote or large study areas), morphological (e.g. absence of individually identifiable traits) and various other aspects of the natural history of an animal. This is typically the case for large carnivores and most threatened or endangered species, but because management objectives are often centred on viable population sizes, statistically defensible abundance estimates remain critical to conservation and recovery programmes.

There has been some success with deriving population estimates for rare and elusive wildlife populations using capture–recapture methods, including both traditional and spatial approaches (Williams, Nichols & Conroy 2002; Royle *et al.* 2009). For example, DNA sampling from hair snares has been effective for brown bears (Kendall *et al.* 2008), while trail cameras have worked for felids with uniquely identifiable fur coloration patterns (Royle *et al.* 2009). However, these methods can be prohibitively expensive and field intensive for abundance estimation across a large geographic range. Furthermore, for species that are difficult to sample using hair snares or species lacking individually identifiable characteristics (e.g. spots or stripes), these techniques cannot be reliably used to estimate population size. One such animal is the endangered Florida panther (*Puma concolor coryi*).

The Florida panther is the only puma subspecies remaining in eastern North America and has been listed as endangered under the US Endangered Species Act for over 40 years (USFWS 2008). Although a species of concern whose conservation status is intrinsically linked to population size, reliable information about Florida panther abundance is lacking across its core reproductive range in southern Florida, USA. Since 1981, Florida panther movement and survival have been monitored using telemetry collars (Onorato *et al.* 2010). Such long-term monitoring provides valuable demographic data, but information about panther abundance has been largely limited to minimum numbers assumed alive (MNA) from counts based on physical evidence (McBride *et al.* 2008). While the MNA method has provided an index for panther managers to assess changes in the population, such indices provide no measures of uncertainty, do not account for variability in detectability or sampling effort and are clearly underestimates of the actual population size due to imperfect detection. Furthermore, researcher access to panther habitat in Florida is largely restricted to public lands. Of the 1.2 million ha that comprise the breeding range, 37% were under private ownership (Kautz *et al.* 2006). Thus, for the broader geographic range of the Florida panther, assessing abundance via

either MNA or capture–recapture will invariably exclude extensive tracts of private lands that are inaccessible to panther biologists.

Despite efforts to reduce the impacts of anthropogenic disturbance associated with roadways intersecting private and public lands, collisions with motor vehicles remain the major source of documented mortality for the Florida panther (Onorato *et al.* 2010; see Fig. 1). To take advantage of this source of data that is already collected as part of routine monitoring, we propose a novel methodology that capitalizes on a tendency for the public to report motor vehicle collision mortalities (MVMs) to government agencies for prominent species of concern, such as the Florida panther, to estimate abundance at a much larger scale than is possible using conventional methods. Using a combination of data sources, including MVMs reported by the public and routine telemetry monitoring data, we produce the first statistically rigorous estimates for the population size of the Florida panther across its entire breeding range from 2000 to 2012. Our case study highlights one of many potential ways by which hitherto underutilized aspects of human–wildlife ecology can be exploited to produce defensible inferences about species distribution and abundance over broad geographic areas.

Materials and methods

Our approach shares some similarities with so-called mark–resight methods (White & Shenk 2001), where a telemetered (or marked) subset of the target population is used to estimate detection probability and adjust counts of unmarked individuals accordingly. However, the key distinctions to our approach are



Fig. 1. This 4–5-year-old male Florida panther was found along State Road 29 in Collier County, Florida, USA, on 1 July 2002. Wildlife officials determined the cause of death to be vehicle collision. Photo credit: David Shindle.

as follows: i) detection probability is not the probability of capturing or sighting a live individual, but rather the probability of a reported MVM; and ii) counts of unmarked individuals are obtained from MVMs reported to wildlife officials by the public. In the same spirit as dead recovery models of survival probability (Brownie *et al.* 1985) or carcass recovery models of mortality rate (Bellan *et al.* 2013), the statistical challenge lies in reliably estimating the probability of a reported MVM.

THE MVM MODEL

We assume the number of marked individuals alive in the study area is known during the period of interest for abundance estimation. Such ‘known-fate’ data typically rely on capture events where marked individuals are fitted with transmitters that allow the location and survival of each individual to be closely monitored (Williams, Nichols & Conroy 2002). We divide the study period into S seasons, each consisting of T_s ($s = 1, \dots, S$) distinct sampling periods. For ease of exposition, we will initially assume the population is geographically and demographically closed within each season (with the exception of losses due to MVMs). If MVM public reporting rates are <100%, this does not pose a significant problem because the known fates of the marked individuals enable estimation of the probability of a reported MVM.

Assuming the marked population is representative of the unmarked population with respect to MVM and public reporting probability, we can modify the logit-normal mark–resight model likelihood (McClintock & Hoeting 2010; McClintock *et al.* 2013) to accommodate MVMs. Letting $y_{s,t,i} = 0$ indicate marked individual i was not a MVM during sampling period t of season s , $y_{s,t,i} = 1$ indicate marked individual i was a reported MVM, and $y_{s,t,i} = 2$ indicate marked individual i was determined by officials to be a MVM event, but this MVM was not independently reported to officials by the public, then

$$L(\mathbf{y}, \mathbf{u} | \boldsymbol{\delta}, \mathbf{r}, \mathbf{U}) = \prod_{s=1}^S \prod_{t=1}^{T_s} \left[\prod_{i=1}^M \text{Categorical}(y_{s,t,i}; \delta_{s,t,i}, r_{s,t,i}) \right] \times \text{Binomial} \left(u_{s,t}; U_s - \sum_{k=1}^{t-1} u_{s,k}, \bar{\delta}_{s,t} \bar{r}_{s,t} \right) \quad \text{eqn 1}$$

where

$$\text{Categorical}(y_{s,t,i}; \delta_{s,t,i}, r_{s,t,i}) = \begin{cases} 1 - q_{s,t,i} \delta_{s,t,i} & \text{if } y_{s,t,i} = 0 \\ q_{s,t,i} \delta_{s,t,i} r_{s,t,i} & \text{if } y_{s,t,i} = 1 \\ q_{s,t,i} \delta_{s,t,i} (1 - r_{s,t,i}) & \text{if } y_{s,t,i} = 2, \end{cases}$$

$u_{s,t}$ is the number of reported MVMs for unmarked individuals, $q_{s,t,i} = 1$ is an indicator for whether individual i was alive and marked at the beginning of period t ($q_{s,t,i} = 0$ otherwise), M is the total number of unique individuals that were alive and marked at the beginning of at least one sampling period during the study, $\delta_{s,t,i}$ is the probability of MVM for marked individual i , $r_{s,t,i}$ is the probability of the public reporting a MVM for marked individual i , and U_s is the unmarked population size during season s . For a randomly selected individual from the population, we have $\bar{\delta}_{s,t} = E_i(\delta_{s,t,i})$ and $\bar{r}_{s,t} = E_i(r_{s,t,i})$. When $r_{s,t,i} = 1 \forall i$, abundance at the end of each season is derived as $N_s = \sum_i q_{s,T_s,i} - \sum_i y_{s,T_s,i} + U_s - \sum_{t=1}^{T_s} u_{s,t}$. When $r_{s,t,i} < 1$ for any

i , the model instead provides a derived estimate of abundance at the beginning of the season: $N_s = M_s + U_s$, where $M_s = \sum_i I(\sum_{t=1}^{T_s} q_{s,t,i} > 0)$ is the number of animals known to be alive and marked at the beginning of season s , and $I()$ is the indicator function.

Clearly, accurate estimation of MVMs and reporting probabilities from the marked population is critical to reliable estimation of abundance. This can be facilitated through the identification and collection of appropriate explanatory covariates for the MVM reporting process, such as temporal, environmental, behavioural or social factors. The logit link can be used to model $\delta_{s,t,i}$ or $r_{s,t,i}$ as a function of covariates, for example $\text{logit}(\delta_{s,t,i}) = \mathbf{x}'_{s,t} \boldsymbol{\beta} + \mathbf{z}'_{s,t,i} \boldsymbol{\alpha}$, where $\mathbf{x}_{s,t}$ is a vector of covariates common to all individuals during period t of season s , $\mathbf{z}_{s,t,i}$ is a vector of k individual-level covariates, and $\boldsymbol{\beta}$ and $\boldsymbol{\alpha}$ are corresponding vectors of regression coefficients. The expected MVM and reporting probability can then be calculated by the k -dimensional integral, for example $\bar{\delta}_{s,t} = \int_z \text{logit}^{-1}(\mathbf{x}'_{s,t} \boldsymbol{\beta} + \mathbf{z}' \boldsymbol{\alpha}) f(z) dz$, where $f()$ is the joint probability density (or mass) function for the individual-level covariates.

In the absence of geographic and demographic closure (e.g. due to movement, recruitment or non-MVM mortality), our approach can be used to estimate the ‘open’ population size using the study area during the period of interest. This is accomplished by incorporating additional states based on the known fates and locations of the marked individuals. For example, suppose demographic closure is violated within seasons due to ‘natural’ (non-MVM) mortality. Although underutilized in wildlife studies, instantaneous rates are commonly used in fisheries science to model competing sources of mortality *sensu* the Baranov catch equation (Baranov 1918; Hoening *et al.* 1998). If we let $y_{s,t,i} = 3$ indicate marked individual i was a natural mortality and assume instantaneous mortality rates are constant within sampling periods, we can modify eqn 1 to accommodate both MVM and natural mortality:

$$L(\mathbf{y}, \mathbf{u} | \mathbf{D}, \mathbf{r}, \mathbf{P}, \mathbf{U}) = \prod_{s=1}^S \prod_{t=1}^{T_s} \left[\prod_{i=1}^M \text{Categorical}(y_{s,t,i}; D_{s,t,i}, r_{s,t,i}, P_{s,t,i}) \right] \times \text{Binomial} \left(u_{s,t}; U_s - \sum_{k=1}^{t-1} u_{s,k}, \frac{\bar{D}_{s,t} \{1 - \exp(-\bar{Z}_{s,t})\} \bar{r}_{s,t}}{\bar{Z}_{s,t}} \right) \quad \text{eqn 2}$$

where

$$\text{Categorical}(y_{s,t,i}; D_{s,t,i}, r_{s,t,i}, P_{s,t,i}) = \begin{cases} q_{s,t,i} \exp(-Z_{s,t,i}) + 1 - q_{s,t,i} & \text{if } y_{s,t,i} = 0 \\ \frac{q_{s,t,i} D_{s,t,i} \{1 - \exp(-Z_{s,t,i})\} r_{s,t,i}}{Z_{s,t,i}} & \text{if } y_{s,t,i} = 1 \\ \frac{q_{s,t,i} D_{s,t,i} \{1 - \exp(-Z_{s,t,i})\} (1 - r_{s,t,i})}{Z_{s,t,i}} & \text{if } y_{s,t,i} = 2 \\ \frac{q_{s,t,i} P_{s,t,i} \{1 - \exp(-Z_{s,t,i})\}}{Z_{s,t,i}} & \text{if } y_{s,t,i} = 3, \end{cases}$$

$D_{s,t,i}$ is the instantaneous MVM rate, $P_{s,t,i}$ is the instantaneous natural mortality rate, $Z_{s,t,i} = D_{s,t,i} + P_{s,t,i}$, $\bar{D}_{s,t} = E_i(D_{s,t,i})$, $\bar{P}_{s,t} = E_i(P_{s,t,i})$ and $\bar{Z}_{s,t} = E_i(D_{s,t,i} + P_{s,t,i}) = \bar{D}_{s,t} + \bar{P}_{s,t}$.

The population using the study area each season is then derived as $N_s = M_s + U_s$. The instantaneous mortality rates can be modelled as functions of covariates using the log link function: for example, $\text{log}(D_{s,t,i}) = \mathbf{x}'_{s,t} \boldsymbol{\beta} + \mathbf{z}'_{s,t,i} \boldsymbol{\alpha}$ and $\bar{D}_{s,t} = \int_z \exp(\mathbf{x}'_{s,t} \boldsymbol{\beta} + \mathbf{z}' \boldsymbol{\alpha}) f(z) dz$.

APPLICATION TO THE FLORIDA PANTHER

We used data collected within the breeding range of Florida panthers, which is restricted to $12\,600\text{ km}^2$ of available habitat in south Florida (Kautz *et al.* 2006; Land *et al.* 2008; Onorato *et al.* 2011). The study area is bordered by the Caloosahatchee River to the north, Florida Bay to the south and the urban areas of Miami-Fort Lauderdale and Naples-Fort Myers to the east and west, respectively (Fig. 2). While the breeding range of panthers within the interior of south Florida has a lower density of roads in comparison with the metropolitan areas along the coastline, there are still numerous state, county and local roads that panthers must cross with regularity. One major U.S. interstate highway (I75) transects the core of panther habitat by connecting Fort Lauderdale and Naples. A 40-mile stretch of this interstate that runs through prime panther habitat has been fitted with continuous high fencing and 36 underpasses specifically built or retrofitted for wildlife (Lotz, Land & Johnson 1997; Onorato *et al.* 2010). This has undoubtedly reduced the number of road mortalities that would have been expected to occur on this high-speed roadway. Despite these efforts, and the construction of wildlife underpasses for panthers in other areas of south Florida, MVM remains the major cause of mortality for panthers documented by agency personnel.

Based on known-fate data for marked panthers and public reports of MVMs for both marked and unmarked panthers, our goal is to estimate the adult and subadult (≥ 1 year old) male and female population sizes of the endangered Florida panther across its breeding range from 2000 to 2012. We relied on two sources of data collected by Florida Fish and Wildlife Conservation Commission (FWC) and National Park Service biologists. The first data source came from panthers that were captured and radiocollared with VHF transmitters (methods described elsewhere; Land *et al.* 2008; FWC 2013). Location data for the marked (*i.e.* radiocollared) panthers were collected during routine aerial monitoring flights three times per week (Land *et al.* 2008). Whenever a radiocollar emitted a mortality signal, researchers would

quickly locate the carcass and determine the cause of death (*e.g.* intraspecific aggression, disease, MVM, unknown). Thus, the number of marked individuals alive in the study area was known during the entire study period. Of the many causes of panther mortality, MVM is arguably the easiest to identify based on characteristic traumatic injuries and the location of the carcass. We are therefore confident that mortalities identified as MVMs were not actually the result of an alternate cause of death and that unknown causes of death were not actually MVMs.

The second source of data was MVMs of both marked and unmarked panthers reported by the public to agency personnel from 2000 to 2012 (Fig. 3). Officials would dispatch to the site to confirm the validity of any report as soon as possible, and 94 unmarked MVMs were reported and confirmed within the study area. The vast majority of marked MVMs (13 individuals) were reported to agency personnel by the public. There were three exceptions where marked MVM carcasses were located through aerial telemetry and removed from the roadside by agency personnel prior to public reporting. Given the location of two of these carcasses when recovered, we believe these carcasses would have eventually been reported to agency personnel. One carcass of a marked MVM was located some distance from the roadway and would not have been found without the assistance of the radiocollar signal. Thus, for the purposes of this analysis, we treated 12 of the 13 marked MVM events as if they had been reported by the public.

MVM events occur year-round in the breeding range of the Florida panther. We divided our data into $S = 13$ seasons corresponding to the 2000–2012 calendar years. We further subdivided each season into 2-month sampling periods (hence $T_s = 6$ for $s = 1, \dots, 13$). Clearly, the population was not closed to recruitment, movement or non-MVM mortality within each season; this necessitated estimation of the population size using the breeding range each year as in eqn 2. However, because it does not explicitly account for movement or recruitment processes, we note that this ‘open’ model is an approximation (but see *Discussion*).

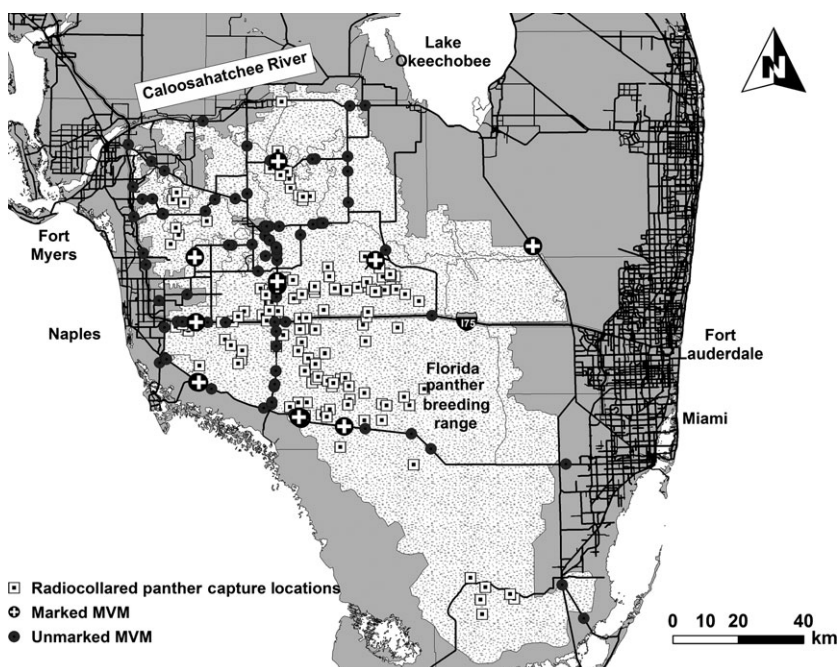


Fig. 2. Delineation of the breeding range of the Florida panther in southern Florida, USA. A 40-mile stretch of U.S. Interstate 75 has been fitted with wildlife underpasses and continuous high fencing to reduce wildlife road mortalities on this high-speed roadway. Squares represent radiocollared panther capture locations, circles with crosses represent motor vehicle mortalities (MVMs) of radiocollared panthers, and dark circles represent MVMs for unmarked panthers.

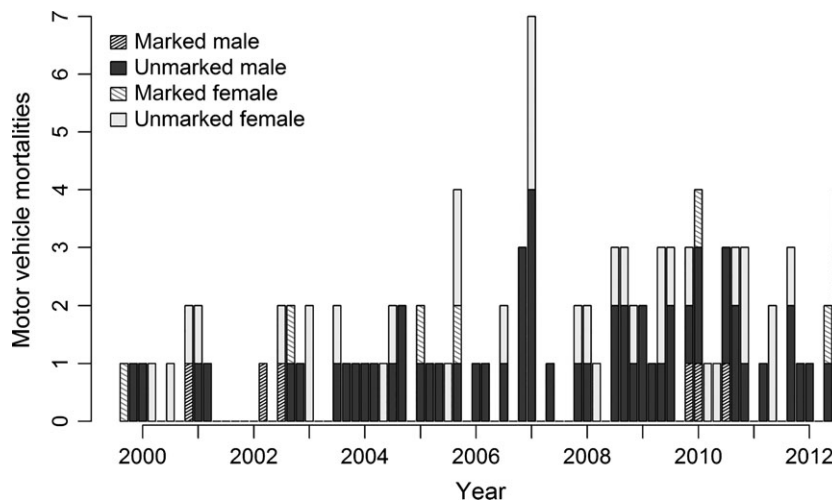


Fig. 3. Motor vehicle mortality (MVM) events for marked and unmarked Florida panthers observed within the study area during each bimonthly sampling period from 2000 to 2012. Marked counts include both reported and unreported MVMs, but unmarked counts include only those reported to wildlife officials by the public.

Radiocollars could fail at any point during the study (e.g. due to battery life), so we considered individuals with functional transmitters as ‘marked’ and those without functional transmitters as ‘unmarked’. An additional complication was that marked individuals were introduced to the population from within-season capture events (primarily during the winter months). We therefore modified eqn 2 to accommodate the addition of marked individuals from within-season marking events as well as sex-dependent parameters (see Appendix S1).

Out of $M_1 = 64$ males and $M_2 = 76$ females marked for some period during the study, 12 were reported MVMs, 1 was an unreported MVM, and 63 were ‘natural’ (i.e. non-MVM) mortalities. A naïve estimate for the bimonthly MVM probability across the entire study is therefore $13 / (\sum_{s=1}^{13} \sum_{t=1}^6 \sum_{g=1}^2 \sum_{i=1}^{M_g} q_{g,s,t,i}) = 0.007$ (SE = 0.002). Similar to other panther studies (Sollmann *et al.* 2013), the sparseness of our data limited the complexity of covariate models for the parameters ($P_{g,s,t,i}$, $D_{g,s,t,i}$, $r_{g,s,t,i}$ and $U_{g,s}$). We investigated simple additive models with combinations of sex, age (on log scale), age at initial capture (on log scale), bimonthly sampling period and year effects on $P_{g,s,t,i}$ and $D_{g,s,t,i}$. To explain the MVM process, we developed an ‘index of risk’ covariate for $D_{g,s,t,i}$ based on traffic volume and road density (see Appendix S2). We also investigated models with no sex, temporal or individual covariates (hereafter ‘constant’ models), as well as an age by sex interaction model for $P_{g,s,t,i}$. Only a single unreported marked individual MVM was observed; hence, only constant models for $r_{g,s,t,i}$ were included (i.e. $r_{g,s,t,i} = r$). With relatively few unmarked individual MVMs reported each year (Fig. 3), we suspected yearly effects on $U_{g,s}$ could be numerically unstable, imprecise and overly sensitive to relatively small fluctuations in $u_{g,s,t}$. We therefore investigated more parsimonious models on $\log(U_{g,s})$, including constant, linear, quadratic and cubic trend models. To examine whether the male and female unmarked populations sizes were similar each year, we also included models that constrained $U_{1,s} = U_{2,s}$.

We standardized continuously valued individual covariates and assumed they are (approximately) normally distributed with mean and variance calculated from the marked individuals: for example, with a single time-invariant individual covariate z_i , $\log(D_{g,s,t,i}) = \mathbf{x}'_{g,s,t,i} \boldsymbol{\beta} + z_i^* \alpha$ and $\bar{D}_{g,s,t} = \int_{-\infty}^{\infty} \exp(\mathbf{x}'_{g,s,t,i} \boldsymbol{\beta} + z^* \alpha) N(z^*) dz^* = \exp(\mathbf{x}'_{g,s,t} \boldsymbol{\beta} + \frac{\alpha^2}{2})$, where $z_i^* = \frac{z_i - \mu_z}{\sigma_z}$, $\mu_z = 1/M \sum_{i=1}^M z_i$, $\sigma_z^2 = 1/(M-1) \sum_{i=1}^M (z_i - \mu_z)^2$ and $N()$ is the standard normal density.

Following the recommendation of Doherty, White & Burnham (2012), we ran all possible combinations of covariate models for MVM rate ($D_{g,s,t,i}$), natural mortality rate ($P_{g,s,t,i}$), unmarked adult male abundance ($U_{1,s}$) and unmarked adult female abundance ($U_{2,s}$). We evaluated the support for each model using Akaike’s information criterion (AIC_c) adjusted for small sample sizes (Burnham & Anderson 2002). Population estimates and unconditional variances for each season were model-averaged based on AIC_c weights, with 95% logarithm-transformed confidence intervals calculated based on a t -distribution with $\sum_{s=1}^S \sum_{t=1}^{T_s} \sum_{g=1}^2 \sum_{i=1}^{M_g} q_{g,s,t,i} + 2 \sum_{s=1}^S T_{s-1} = 2135$ degrees of freedom. All analyses were performed in R (R Core Team 2013) using maximum likelihood methods, and variances for derived parameters were approximated using the delta method. Data and R code to perform our analysis are provided in Data S1.

Results

With 9% of the AIC_c weight, the best-supported model included the risk covariate and bimonthly variability in MVM rate ($D_{g,s,t,i}$), an age by sex interaction on natural mortality rate ($P_{g,s,t,i}$), a (log scale) quadratic trend model for the unmarked male population ($U_{1,s}$) and a (log scale) linear trend model for the unmarked female population ($U_{2,s}$). The estimated bimonthly reporting probability ($r_{s,t}$) from this model was 0.93 (SE = 0.07). This model estimated lower MVM rates from July to October and greater MVM rates in late spring (May to June) and early winter (November to December), with $D_{g,s,t,i}$ increasing with our risk covariate (Fig. 4). Sex- and age-dependent estimates for natural mortality rate ($P_{g,s,t,i}$) from this model are reported in Appendix S3.

There was considerable model selection uncertainty across the 1905 fitted models, but 98% of the AIC_c weight was allocated to models including the risk covariate on MVM rate and an age by sex interaction on natural mortality rate (see Appendix S4). With a model-averaged logit regression coefficient $\beta = 0.75$ (SE = 0.03) for the risk covariate, we found overwhelming evidence that MVM rate increases as a function of road length and AADT volume within a panther’s home range. We found no evi-

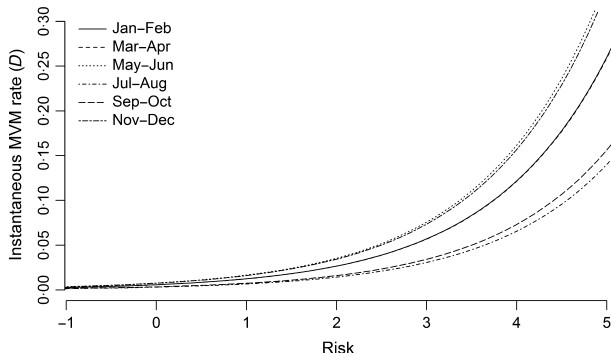


Fig. 4. Minimum AIC_c model estimates of bimonthly motor vehicle mortality (MVM) rate for Florida panthers from 2000 to 2012 as a function of the standardized index of risk covariate. The standardized index of risk covariate had an observed range from -0.8 (lowest risk) to 4.9 (highest risk) for marked panthers.

dence for constant, sex, age or yearly effects on MVM rate. There was some uncertainty about the best model for MVM rate, with 62% of the AIC_c weight allocated to models for $D_{g,s,t,i}$ that included both risk and bimonthly variability, but the primary source of model selection uncertainty was attributable to the unmarked population trend models. For males, quadratic (46% of AIC_c weight), linear (34%) and cubic (18%) trend models received the most support. For females, linear (38%), constant (29%), quadratic (20%) and cubic (13%) trend models received the most support. We found virtually no AIC_c support for models with year-dependent effects on unmarked abundance, with 0.1% and 0.0% of the AIC_c weight for males and females, respectively.

Model-averaged abundance estimates suggest an increasing then stabilizing adult male panther population and a slightly increasing or stabilizing adult female panther population from 2000 to 2012 (Fig. 5). However, with an average annual coefficient of variation of 29% (SE = 0.01), these changes in population size from 2000 to 2012 were not statistically different based on 95% confidence interval overlap. Although confidence intervals do

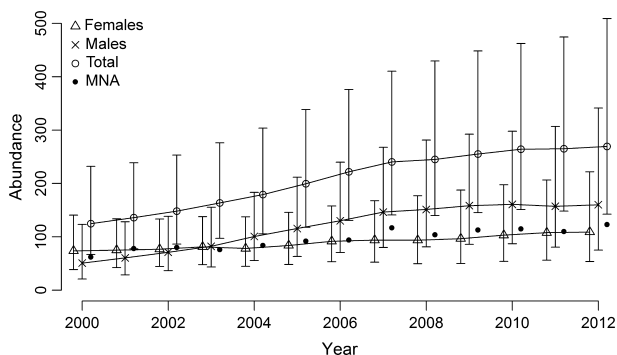


Fig. 5. Annual estimates for the subadult and adult (≥ 1 year old) Florida panther population size using the breeding range from 2000 to 2012. Separate estimates are provided for male and female populations. Total counts for the minimum number assumed alive (MNA) based on physical evidence (McBride *et al.* 2008) are included for comparison.

not suggest a difference between the annual population estimates for males and females, we found little support for the constrained models assuming equal unmarked population sizes for males and females (16% of total AIC_c model weight).

Discussion

We have capitalized on a tendency for the public to report MVMs of species of concern to estimate the population size of an endangered animal that has heretofore been impossible due to logistical constraints commonly encountered for rare, cryptic and broad-ranging species. In addition to public reporting of MVMs, our methodology relies on routine telemetry monitoring that allows the location and survival of a marked subset of the population to be closely followed, thereby allowing estimation of MVM and reporting probability. By relying on the public for sampling the unmarked segment of the population, our methodology comes at little additional cost to ongoing telemetry studies. By relying on the broad network of roads throughout the breeding range of the Florida panther, we demonstrated how our approach facilitates sampling of a much larger geographic area that would otherwise be impractical or inaccessible (e.g. private land) for researchers using more expensive and field-intensive alternatives that rely on live capture or cameras for sampling the unmarked segment of the population (e.g. Sollmann *et al.* 2013). For rare and elusive species that are very difficult to sample using conventional methods, we believe this framework holds much promise for producing defensible estimates of abundance (and its uncertainty) from limited and unconventional sources of data.

Our approach shares some similarities with mark-resight methodology (e.g. White & Shenk 2001). Similar to mark-resight, the most fundamental assumption of our approach is that marked individuals are representative of the entire population in terms of MVM probability, MVM reporting probability and natural survival probability. This assumption is often violated in standard mark-resight studies whenever there is individual variation in sighting probabilities and the marked population is selected based on sightability (McClintock & Hoeting 2010). This was not the case for our study because the marked population was established through capture events (not MVM events). Random or systematic sampling of individuals for marking is difficult to achieve in practice, but efforts can be made at the design stage to help achieve a suitably representative sample. In our case, marked panthers were captured within the large parcels of public lands that support panthers throughout the breeding range. In terms of MVMs and natural survival rates, we have no reason to suspect our marked animals differed from unmarked individuals beyond the individual variation that can be explained by factors such as age, sex and risk covariate. If panthers maintained very small home ranges and were always marked near roads with high

MVM risk (or within protected areas with low MVM risk), then this could induce bias in our abundance estimator. Although panthers were marked on public lands that tend to have fewer roads than private lands, marked panthers did not obey these boundaries (i.e. they were frequently observed on private land).

It is conceivable that the presence of a telemetry collar could affect the MVM reporting rate. A motorist who strikes a collared panther could be more likely to report the incident in the interest of science, but could also be less likely to report out of (unfounded) fear of recrimination. Given the volume of motor vehicle traffic on the roads of southern Florida and the prominence of panthers with the public, we would only expect different MVM reporting probabilities for marked panthers if motorists were consistently attempting to hide marked carcasses from view. We presently have no evidence in support of such a scenario. Because we had no reason to suspect otherwise, MVM reporting probability was assumed to be constant over time. Although we considered models that included both bimonthly and annual variation in MVM rate, the best-supported models assumed no annual variation. This may be explained by the sparseness of the data.

By relying on a representative sample of marked individuals selected independently of the sighting process, mark–resight methods do not require that the area searched be the entire study area (Bowden & Kufeld 1995). Individual variation in MVM probability (e.g. due to road density) does not induce bias in abundance point estimates, but if not accounted for, its uncertainty can be underestimated. We therefore used a surrogate for sampling intensity (i.e. road length and traffic volume) to help explain individual variation in MVM probability. Although annual road length and traffic volume data were unavailable for our study, it could be important to account for temporal trends in these covariates for long-term population monitoring. For example, if human development and population growth leads to increases in road density and traffic volume in some areas during the course of a study, so too may the MVM risk for individuals with home ranges that include these areas.

Given the sparseness of the panther MVM data, we found overwhelming support for (log scale) trend models on the unmarked population sizes. We found the most support for increasing linear or quadratic trend models for the unmarked male population and increasing linear trend or stable models for the unmarked female population. Although these trend models proved more parsimonious and yielded more stable estimates than the most general year-dependent models, the biological interpretation of these models requires additional care. Trend models on the unmarked population size can only be interpreted as the overall population trend if the number of marked individuals remains relatively constant or is a small proportion of the total population. The number of marked panthers in our study was relatively constant due

to similar winter capture efforts each year, with the number of marked males ranging from 10 to 17 per year (median = 13, SD = 2.3) and the number of marked females ranging from 10 to 25 per year (median = 20, SD = 4.9).

We made several modifications to the ‘closed’ population model (eqn 1) to accommodate a lack of demographic and geographic closure within each year of the panther study. However, our ‘open’ model for the panther population using the study area each year is still approximate because it does not explicitly account for the within-year movement or recruitment processes. For example, an unmarked individual recruited to the adult population in November is (incorrectly) treated as if it had been present for the entire year by our approximate likelihood. A single marked male permanently emigrated north of the breeding range, but we did not observe any temporary emigration on or off the breeding range by marked panthers. Given that panthers persist as a single, isolated breeding population in south Florida, we had little to no concern about potential biases induced by immigrants moving into the study area from another population. However, we investigated the potential biases induced by within-season *in situ* reproduction through simulation experiments. We found our approximate likelihood performed well for a realistically simulated population under similar sampling conditions to the panther study, with negligible bias (-0.1%) and near-nominal 95% confidence interval coverage (92.1%) of open population abundance (see Appendix S5).

Because the panther population was not closed, the population using the study area each year is clearly larger than the actual population within the study area at any given point in time. Our open population estimates are therefore inappropriate for inferences about panther density. Lack of geographic closure can be readily handled under our framework to produce estimates suitable for density (McClintock & White 2012), but natural mortality and *in situ* reproduction pose additional challenges for estimating population density. It may be possible to utilize auxiliary demographic information to estimate panther density using post hoc analysis or integrated population modelling (e.g. Conn *et al.* 2008); this is the focus of additional research.

In eqns 1 and 2, we effectively assume that carcasses persist long enough to be reported with nonzero probability during the sampling period in which the MVM event occurred. All reported MVMs for marked panthers occurred within days of the MVM event, and given the size of the carcasses, the persistence rate of panthers on roadways is likely to be very high. However, this may not be the case for smaller species or other carcass recovery programmes. Unreportable carcasses arising from removal (e.g. due to scavenging) or degradation (e.g. due to decomposition) result in r being redefined as a combined ‘persistence and reporting’ probability in eqns 1 and 2, but this is not a problem for abundance estimation

because all unmarked encounters consist of carcasses that both persisted and were reported. For example, the estimator does not necessarily need to distinguish unreported MVMs that were intact but obscured behind roadside vegetation from those that were dragged off the roadway by scavengers (but it is certainly possible to do so). However, when reporting rates are low and the duration of the sampling period is short relative to carcass persistence, then our modelling approach may not be appropriate because we assumed that mortality events occurred during the sampling period in which they were observed.

MANAGEMENT IMPLICATIONS FOR THE FLORIDA PANTHER

Our Florida panther abundance estimates suggested the adult population has increased across its core reproductive range over the past decade, with possible stabilization in recent years. Despite low MVM probabilities, we achieved an average coefficient of variation of 29%. This precision is reasonable and similar to other panther studies (Sollmann *et al.* 2013). However, our model-averaged confidence intervals were still too large to conclude there were significant increases in population size from 2000 to 2012. Furthermore, upper confidence interval bounds in later years (e.g. 509 panthers in 2012) exceeded population estimates we believe could be supported within the breeding range of the Florida panther. These higher upper bounds are likely an artefact of a low MVM probability, which was about 0.04 (SE = 0.01) annually during our study. Although we chose to let these data 'speak for themselves', additional model structure could incorporate information about the carrying capacity of the breeding range.

Perhaps most informative are the estimated lower bounds for the annual population estimates for the panther breeding range. As expected, we consistently found the lower bounds exceeded MNA counts based on physical evidence (see Fig. 5), but our annual population estimate generally follows the same trend as the MNA method through the course of the study period. Progress associated with recovery of critically endangered animals should preferably rely on conservative measures of population estimates or lower bounds, especially when data are sparse due to the challenges of monitoring rare species (Miller & Waits 2003; Mills 2007). Our estimated lower bounds indicate this single population may never have exceeded 150 individuals between 2000 and 2012. As part of the recovery criteria for the Florida panther, three distinct populations of 240 individuals must be established before delisting. Two distinct populations of 240 individuals must be maintained for two panther generations (12 years) to downlist the subspecies to threatened. Although our results do not support a change in listing status for the Florida panther based on these established recovery criteria, they do suggest that management initiatives (e.g. genetic restoration, wildlife underpasses and corridors) to this point appear to be working. Our

methodology can be continually applied on an annual basis at little additional cost and could help alert managers if the population appears to be declining, stabilizing or continuing to increase.

A novel methodology recently introduced by Chandler & Royle (2013), which we refer to as spatial mark-resight, was recently investigated for estimating Florida panther density using trail cameras (Sollmann *et al.* 2013). Although very useful and promising, the estimates of Sollmann *et al.* (2013) were limited to 2 years on a relatively small study area (241 km²) on public land. Even if access to private lands was unrestricted, it would likely be prohibitively expensive and field intensive to continuously monitor panther density over its entire range using spatial mark-resight. In addition to routine telemetry monitoring, spatial mark-resight incurs substantial camera, field vehicle, fuel, battery and labour costs. Our approach utilizes data that are already collected as part of routine monitoring, and its costs are therefore negligible in comparison. However, we ultimately believe the most precise and cost-effective approach for continued monitoring across the entire breeding range of the Florida panther will combine all sources of available information (e.g. spatial mark-resight and mark-recapture, MVM, telemetry, recruitment data) in a spatially explicit integrated population model (e.g. Chandler & Clark 2014).

Our abundance model was developed for historical data that were originally collected for purposes other than population size estimation. Despite a sparse data set, we were able to obtain useful information about abundance of panthers while accounting for imperfect detection. This is a substantial improvement compared to indices of abundance derived from uncorrected minimum counts (e.g. MNA). Should researchers wish to pursue our methodology for other species as a less expensive means for long-term population monitoring, we suggest a focus on improving precision by devoting additional resources to maintaining a relatively large pool of marked (i.e. radio-collared) individuals in their focal population. Sample sizes for unmarked individuals could also potentially be increased through awareness campaigns encouraging the public to report encounters with wildlife. Of course, there are cost-benefit trade-offs that practitioners must consider when attempting to increase sample sizes under this framework.

Although initially developed for the Florida panther, our methodology is not limited to this particular species or aspect of human-wildlife ecology. Because it relies on citizen-based science, our technique could be adapted for any population that is encountered by a reporting public and contains a subset of closely monitored marked individuals. Harvested populations are an obvious example, although these studies will typically have sufficient recovery data to support more complicated modelling approaches than proposed here (e.g. Conn *et al.* 2008). Other examples include reports of avian wind farm collisions, beached whales or marine mammal boat strikes, which conceivably could be

utilized under this framework for long-term population monitoring over broad geographic areas.

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Data accessibility

Panther data: uploaded as online supporting information. R scripts: uploaded as online supporting information

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Supporting Information

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

Appendix S1. Modified likelihood.

Appendix S2. Index of risk covariate.

Appendix S3. Natural mortality rates.

Appendix S4. Model selection.

Appendix S5. Simulation study.

Data S1. Data and R code.