

Maned wolf survival rate in central Brazil

R. Sollmann^{1,2}, M. M. Furtado^{1,3}, A. T. A. Jácomo¹, N. M. Tôrres^{1,4} & L. Silveira¹

¹ Jaguar Conservation Fund/Instituto Onça-Pintada; Mineiros, Brazil

² Leibniz Institute for Zoo and Wildlife Research; Berlin, Germany

³ Departamento de Medicina Veterinária Preventiva e Saúde Animal, Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, São Paulo, Brazil

⁴ Universidade Federal de Goiás, Departamento de Biologia Geral; Goiânia, Brazil

Keywords

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Correspondence

Rahel Sollmann, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Strasse 17, 10315 Berlin, Germany.
Email: rahel.sollmann@jaguar.org.br

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Abstract

Although many carnivores are of conservation concern, most are poorly studied. The maned wolf *Chrysocyon brachyurus* Illiger, 1811 is the largest South American canid with a broad distribution; however, the largest portion of its range is in the Brazilian Cerrado savannah, where due to intensive agricultural expansion, it is threatened by habitat loss. Maned wolf population trends are virtually unknown. We analyzed radio telemetry data from a 13-year study in Emas National Park, central Brazil, with Burnham's live recapture/dead recovery models in the program MARK to obtain the first analytically sound estimate of the apparent maned wolf survival rate. We constructed 16 candidate models including variation in survival rate and resighting probability associated with an individual's sex or age and year of study. Apparent adult survival rate throughout the study ranged from 0.28 (SE = 0.08) to 0.97 (SE = 0.06). There was no evidence for sex specificity but strong support for time variation. Model weights supported an age effect and the subadult survival rate was 0.63 (SE = 0.15). Results indicate similar life patterns for male and female maned wolves and similar mortality risks for adults and subadults in the study area. The observed temporal fluctuations of adult survival rate are important for population dynamics as they decrease average population growth rates. Population dynamics are central for conservation planning and our results are an important step towards a better understanding of the maned wolf's ecology.

Introduction

Among terrestrial mammals worldwide, several of the most threatened species are carnivores (Ceballos *et al.*, 2005; Schipper *et al.*, 2008). Their high potential for conflict with humans – as competitors for food and space or as a threat to livestock or human lives – turns carnivore conservation into a difficult task. As they generally occur at low densities and have elusive habits, several species remain poorly studied. This lack of information hampers conservation efforts and there is a need for ecological knowledge of individual species (Karanth & Chellam, 2009).

Information about abundance and demographic parameters is crucial in guiding conservation and management (Lebreton *et al.*, 1992; Reid *et al.*, 2002). These parameters allow characterization of a species' past and current population status, and when used in a population viability analysis framework, they can even provide insight into future population trends under various environmental and management scenarios (Beissinger, 2002). However, obtaining reliable estimates of abundance and vital rates is challenging due to methodological difficulties in studying rare and/or elusive

species (Karanth & Chellam, 2009). In addition, investigating population dynamics requires long-term studies (Beissinger, 2002), which are often difficult to fund. As a result, information about population dynamics is scarce or absent for several large carnivores (Karanth *et al.*, 2006).

The maned wolf *Chrysocyon brachyurus* Illiger, 1811 is the largest South American canid, with a mean shoulder height of 90 cm and a mean weight of 23 kg (Eisenberg & Redford, 1999). The species is found in Brazil, Paraguay, eastern Bolivia and northern Argentina (Langguth, 1975) and lives in monogamous breeding pairs that inhabit exclusive pair territories (Dietz, 1984; Rodrigues, 2002; Jácomo *et al.*, 2009). Home-range size varies among studies, from 30 km² (Dietz, 1984) up to 80 km² (Jácomo *et al.*, 2009), and the few existing estimates indicate low population densities between 1.56 and 5.19 individuals/100 km² (Trolle *et al.*, 2007; Silveira *et al.*, 2009).

The Brazilian savannah, or Cerrado, constitutes the largest portion of the species' range (Rodden, Rodrigues & Bestelmeyer, 2004) and is thought to harbor > 20 000 maned wolves (Paula, Medici & Morato, 2008). The Cerrado is Brazil's second largest biome covering 21% of the country's

area (Klink & Machado, 2005); however, this biome, identified as one of the 25 ecological hotspots of the earth (Myers *et al.*, 2000), suffers strong anthropogenic pressures. Over the last 35 years, more than half of the Cerrado has been transformed into agriculture and cattle pasture (Klink & Machado, 2005) and 80% is considered to be degraded. Only 1.9% of its area is under strict protection (Cavalcanti & Joly, 2002). Thus, in spite of the maned wolf's broad distribution and Near Threatened classification (IUCN, 2009), the species faces a serious threat of habitat loss (Paula *et al.*, 2008). Yet, virtually nothing is known about population trends (Rodden, Rodrigues & Bestelmeyer, 2008).

We used 13 years of radio telemetry data on maned wolves from the region of Emas National Park (ENP), an important refuge for the species, and open population mark–recapture models to present the first analytically sound estimate of the species' survival rate.

Study area

Emas National Park, located in central Brazil in southwestern Goiás state (18° 19'S, 52° 45'W; Fig. 1), lies in the centre of the maned wolf's distribution. Large tracts of grassland plains (97%), small patches of shrub fields (1%), marshes and riparian forest (2%) are protected in this 132 000 ha area, which is listed as a Human Heritage Reserve by UNESCO. During the wet season (October–March), precipitation averages 1500 mm. Virtually no rainfall occurs during the rest of the year, when daytime temperatures may reach 40 °C and night temperatures may drop as low as –1.5 °C (IBDF/FBCN, 1981). ENP is situated in a highly productive agricultural area, and large-scale soybean, corn and sugar cane plantations dominate

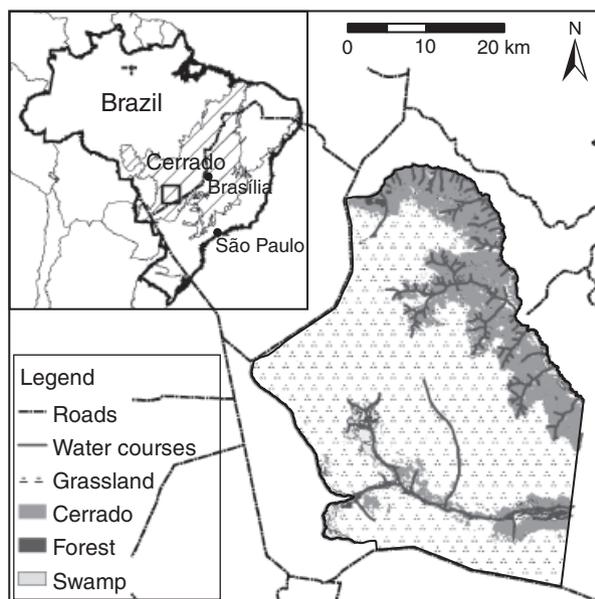


Figure 1 Location of Emas National Park in the Cerrado savannah of Brazil (square in inset) and habitat map of the Park.

and fragment the regional landscape. The study was carried out both within ENP and on private properties in the immediate surroundings.

Material and methods

From 1995 until 2007, we captured 72 maned wolves in ENP and its surroundings (Fig. 2) and equipped them with radio collars with mortality signal. Of these individuals, 63 were adults (>2 years) and nine were subadults (1–2 years, fully grown but generally not reproductively active; Rodden *et al.*, 2004). Because radio-collaring is only appropriate for fully grown individuals, we were unable to include younger age classes in our study. We monitored all collared individuals for home-range estimation (for details, see Jácomo *et al.*, 2009) and aimed at recapturing individuals annually for collar change. Collars activated a mortality signal if no movement was detected over two continuous hours.

We analyzed telemetry data using the combined recapture/recovery models (Burnham, 1993) in program MARK (White & Burnham, 1999) to obtain an estimate of the annual maned wolf survival rate. These mark–recapture models accommodate the use of both live resighting (or recapture) and dead recovery data, generally leading to better estimates of survival rate than models using only one data type (Burnham, 1993). Live resighting is assumed to occur during discrete events of short durations, while recovery can occur at any point during the intervals between resighting events. We used successful radio-telemetry location of an animal in a given year as live resighting data, and confirmed mortality of an animal as recovery data. As we monitored maned wolves continuously, our resighting data are continuous rather than discrete and intervals between resightings do not necessarily correspond to a year. In treating resighting as a discrete yearly event, we may over- or underestimate annual survival, depending on whether the true intervals are shorter or longer than 1 year, respectively. While there are specific estimation methods for continuous

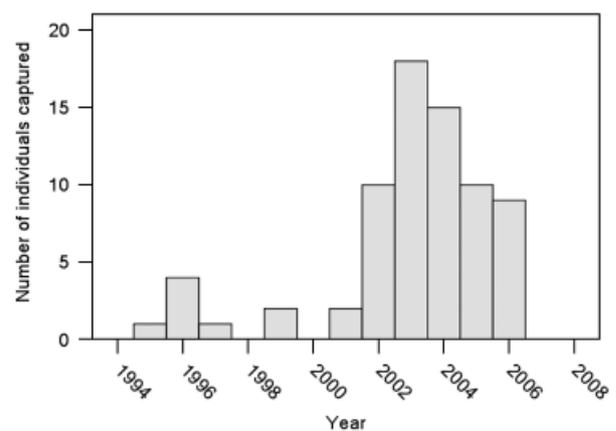


Figure 2 Number of maned wolves *Chrysocyon brachyurus* newly captured and subsequently radio-monitored in Emas National Park for each year of the present study.

data, the discrete data capture–recapture analysis allows a separate estimation of resighting and survival probability (Murray & Patterson, 2006). This is necessary when an animal is not resighted, although alive and in the study area (resighting probability < 1), which is the case in the present study. Both continuous and discrete time approaches tend to yield similar results (Murray & Patterson, 2006).

Under the parameterization implemented in MARK, combined recapture/recovery models estimate four parameters: survival rate (S), site fidelity (the probability that an animal does not permanently emigrate from the sampled area) conditional on survival (F), probability of resighting (P) conditional on being alive and in the study area and probability of recovery (r) (White & Burnham, 1999). Site fidelity can only be estimated if dead animals are recovered from an area larger than that where live encounters occur. Indeed, it is usually assumed that animals cannot move to areas where recovery is impossible. Only then, the combined model is able to estimate true survival (Burnham, 1993). In our case, the areas sampled for resighting and recovery were identical ($F = 1$). Thus, we estimated apparent rather than actual survival and in the remainder of the text use ‘survival rate’ synonymously for ‘apparent survival rate’.

We built a set of 16 candidate models using the following sources of parameter variation and notations: we assumed S could be constant (\cdot) or vary with time (t), due to fluctuations of environmental factors; with age (age), as subadults generally suffer higher mortality during dispersal (Dietz, 1984; Paula *et al.*, 2008); and with gender (sex), as males appear to play a more dominant role in territory defense (Dietz, 1984), thus being potentially exposed to higher degrees of aggression and/or stress. However, overall, maned wolves show little sexual dimorphism in their behavior or ecology (e.g. similar home-range size, both sexes involved in parental care; Dietz, 1984; Jácomo *et al.*, 2009), and we assumed that external factors influence survival for both genders similarly. Thus, we modeled sex as an additive effect in time and sex-dependent models ($t + \text{sex}$). We assumed that r could be constant (\cdot) or differ with age (age), as juveniles have a higher probability of dispersing from the study area, resulting in an effective $r = 0$. When captured as subadults in year y , individuals were considered adults at $y + 1$. Whenever we assumed age dependence in S , we held S for subadults constant (no variation with sex or time), due to the low number of subadults monitored. We held P constant, as monitoring effort was comparable over the years and for all individuals, and the raw data indicate this parameter to be constantly close to 1.

We also applied some restrictions to our models that arose from data collection: compared with later years, the dataset from the first 7 years is small (only 10 individuals captured/monitored, Fig. 2) and contains no information about dead recoveries (these might have happened but were not recorded). Therefore, we fixed $r = 0$ and held the other parameters constant over this period. As such a small dataset does not support the estimation of many parameters (Burnham & Anderson, 2002), we used this approach as an alternative to excluding these data completely.

To check for an overall goodness of fit (GOF) of our model, we built a fully time-dependent Cormack–Jolly–Seber (CJS) model and used the χ^2 -tests implemented in program U-CARE V2.3 (Choquet *et al.*, 2008). This program uses four partial tests (TEST3.SR, TEST3.SM, TEST2.CT and TEST2.CL) to detect the violation of general model assumptions of homogeneity in recaptures and independence of individuals that apply to the CJS model (Choquet *et al.*, 2005), which effectively constitutes the live resighting component of the combined model we used.

We used the Akaike Information Criterion adjusted for small samples (AICc; Burnham & Anderson, 2002) to choose the best-fitting models from our set of candidate models. MARK also estimates AICc weights, indicating the support for a model relative to all other candidate models. To consider uncertainty in model choice, we present model-averaged parameter estimates (weighted averages based on AICc weights) with their standard errors (SE) (Buckland, Burnham & Augustin, 1997). Following recommendations by Burnham & Anderson (2002), we considered all models with an AICc within 2 units of the best-fitting model’s AICc as being substantially supported. For adult S , we further report SD due to process variation. Process variation reflects the actual temporal variation in survival rate, excluding variation due to sampling (i.e. the uncertainty that arises from estimating parameters from a sample of the studied population). Failure to account for sampling variation leads to overestimation of temporal variation in survival rate (Gould & Nichols, 1998). This parameter is calculated by MARK separately for each model containing time dependence in the parameter of interest.

Results

On average, we monitored each of the 72 radio-collared individuals for three years (range: 1–6 years). We confirmed the year of death for 23 individuals. U-CARE could not perform two of the goodness-of-fit tests (TEST2.CT and TEST2.CL) due to sparse data. The remaining tests did not indicate lack of fit of the fully time-dependent CJS model (TEST3.SR: $\chi^2 = 0.443$, $P = 0.979$, TEST3.CL: $\chi^2 = 0.475$, $P = 0.491$). As both TEST2 investigate the presence of a trap response (i.e. differences in first capture and recapture; Choquet *et al.*, 2005) and we do not expect any behavioral response to locating an animal through radio telemetry, we assume that our data fulfilled general model assumptions.

From our 16 candidate models, four received substantial support and thus contributed to model-averaged parameter estimates (Table 1). All supported models included time dependence of S but no effect of sex (Table 1). The best-fitting model that included sex had a ΔAICc of 2.14 (Table 1). However, this value is very close to 2 and the model received some support in terms of model weight. In order not to wrongly discard sex as a factor influencing S , we confirmed the estimate of effect size (beta) of sex given by MARK for this particular model. The beta value for sex was -0.14 (SE = 0.41) and its 95% confidence interval largely overlapped 0 (-0.9477129 , 0.6733075). Therefore, the effect

Table 1 Mixed resighting/recovery models to estimate maned wolf *Chrysocyon brachyurus* survival rate from 13 years of radio-telemetry data in Emas National Park

Model	ΔAICc	AICc weights	Model likelihood	Number of parameters
$\{S(t), r(\cdot)\}^a$	0.00	0.30	1.00	9
$\{S(t, \text{age}), r(\cdot)\}^a$	0.60	0.22	0.74	10
$\{S(t), r(\text{age})\}^a$	1.56	0.14	0.46	10
$\{S(t, \text{age}), r(\text{age})\}^a$	1.97	0.11	0.37	11
$\{S(t+\text{sex}), r(\cdot)\}$	2.14	0.10	0.34	10
$\{S(t+\text{sex}, \text{age}), r(\cdot)\}$	2.57	0.08	0.28	11
$\{S(t+\text{sex}), r(\text{age})\}$	4.41	0.03	0.11	11
$\{S(t+\text{sex}, \text{age}), r(\text{age})\}$	4.86	0.03	0.09	12
$\{S(\cdot), r(\text{age})\}$	15.05	0.00	0.00	4
$\{S(\cdot), r(\cdot)\}$	19.01	0.00	0.00	3
$\{S(\text{sex}), r(\cdot)\}$	20.36	0.00	0.00	4
$\{S(\text{age}), r(\cdot)\}$	20.42	0.00	0.00	4
$\{S(\text{sex}), r(\text{age})\}$	21.33	0.00	0.00	5
$\{S(\text{age}), r(\text{age})\}$	21.38	0.00	0.00	5
$\{S(\text{sex}, \text{age}), r(\cdot)\}$	21.71	0.00	0.00	5
$\{S(\text{sex}, \text{age}), r(\text{age})\}$	22.64	0.00	0.00	6

For all models site fidelity (F) = 1 and resighting probability (P) is constant. Survival rate (S) is constant and recovery rate (r) is 0 over the first 7 years of the study. S is held constant for subadults in models where age-dependence is assumed.

^aModels contributed to model-averaged parameter estimates.

Table 2 Model-averaged parameter estimates of apparent survival rate (S) and recovery rate (r) for maned wolves *Chrysocyon brachyurus* from 13 years of radio-telemetry data from Emas National Park

Parameter	Age class	Year of study	Estimate (SE)
S	Adults	1–7	0.60 (0.13)
		8	0.97 (0.06)
		9	0.83 (0.07)
		10	0.70 (0.07)
		11	0.85 (0.07)
		12	0.28 (0.08)
		13	0.31 (0.38)
r	Subadults	1–13	0.63 (0.15)
	Adults	8–13	0.38 (0.07)
P	Subadults	8–13	0.25 (0.18)
	Adults/subadults	1–13	0.86 (0.04)

For all models site fidelity (F) was fixed at 1. S was constant and r was 0 over the first 7 years of the study. For subadults, S was held constant.

of sex on survival is inconclusive and in our data, it is negligible.

Adult survival rates for both genders fluctuated with a maximum of 0.97 (SE = 0.06) in year 8 and a minimum of 0.28 (SE = 0.08) in year 12 (Table 2). Across the substantially supported models, SD of adult S due to process variation with time ranged from 0.06 to 0.07, corresponding to approximately 22% of the total standard deviation. Model choice showed some evidence of age specificity in S (Table 1), but subadult S (0.63, SE = 0.15) was within the range of that for adults.

Resighting probability (P) was 0.86 (SE = 0.04). For the years 8–13, r was 0.25 (SE = 0.18) for subadults and 0.38 (SE = 0.07) for adults.

Discussion

We evaluated the effect of sex, age and time on maned wolf survival rate in central Brazil. We did not find differences in survival rate between males and females. As maned wolves of both genders show similar ranging and territoriality behavior (Jácomo *et al.*, 2009), our results further corroborate similar life patterns of both sexes. The absence of a sex effect on survival rate has also been observed for other similar-sized canids (e.g., wolves – Marucco *et al.*, 2009; coyotes – Chamberlain, 2001; Kamler & Gipson, 2004; Van Deelen & Gosselink, 2006).

Adult survival rates showed a strong temporal variation. Estimates ranged from 0.28 to 0.97, with a considerable

decline in years 12 and 13 of our study (Table 2). We cannot explain this result satisfactorily – neither did we observe any event impacting the maned wolf population nor was the study conducted differently in these years. In this context, one has to bear in mind the large contribution of sampling variance to the variation in survival rate.

Still, process variation accounted for almost a quarter of the variation in adult survival rate. Process variation in S is caused by random variation in individual fitness (demographic stochasticity) and changes in physical or biological factors affecting the fitness of all individuals of a given population (environmental stochasticity; Lande, 2002) and plays an important role in population dynamics: the stronger the variation over time, the lower a population's persistence (Boyce, 1992). However, reliable estimates of process variation require measurements of demographic parameters over several years (Beissinger, 2002; Lande, 2002). Our estimates of process variation for adult survival rates may be too low, as they are based on 6 years only. It is likely that subadult survival rate underwent similar fluctuations, but due to a small sample size, we were unable to investigate this.

There seems to be no clear pattern concerning annual fluctuations in survival rates for other canids, as they are sometimes observed (e.g. coyotes, Van Deelen & Gosselink, 2006) and sometimes not (e.g. wolves, Marucco *et al.*, 2009). We believe that habitat changes in the area surrounding ENP potentially play a role in the variation of adult maned wolf survival observed. The regional agricultural landscape is very dynamic: plantations change from low-growth plantations such as soy bean and cotton, all usable to some extent by open-habitat species like the maned wolf, to tall-growth plantations such as corn or other cereals that might constitute barriers to open-habitat species. If large areas previously used by maned wolves for foraging temporarily become unavailable, the resulting decrease in food availability could affect survival rate. Also, over the last years, the amount of sugar cane plantations in the study region has increased – again, a tall-growth species – which could have contributed to the decline in the adult survival rate toward the end of the study. However, only investigations on food availability and maned wolf foraging habits in the different agricultural habitat types could show whether this relationship indeed exist.

Although there was support for a difference in survival rates between age classes, subadult survival rate (0.63) was within the range of estimates for adults (Table 2). Generally, subadults are thought to be exposed to increased mortality risks during dispersal and when trying to establish a territory (Dietz, 1984; Paula *et al.*, 2008). An age effect on survival has been shown for wolves (Hayes & Harestad, 2000; Marucco *et al.*, 2009) and coyotes (Van Deelen & Gosselink, 2006), but not consistently in all studies (e.g. for wolves, see Adams *et al.*, 2008). As with apparent survival, subadults dispersing from the study area appear as 'dead', our results could indicate low dispersal from the study area. Emas National Park is comprised of prime maned wolf habitat (Jácomo, Silveira & Diniz-Filho, 2004), and maned wolves use the surrounding farm land extensively. Under the hypothesis that dispersal is largely triggered by resource

competition (Lambin, Aars & Piertney, 2001), there may be only weak dispersal pressure. On the other hand, dispersing individuals may have a lower probability of being captured. In this case, we may have predominantly captured non-dispersing subadults, resulting in an estimate of S that is not representative of the entire age class.

The only other estimate of survival rate for maned wolves, based on expert opinion from a Population and Habitat Viability Analysis for the species, is 0.9 for adults and 0.8 for subadults; road mortality supposedly reduced subadult survival rate to 0.6 (Paula *et al.*, 2008). Emas National Park is bordered by a regional highway, where about five maned wolves are killed on the road annually out of a population of at least 60–70 individuals (Silveira *et al.*, 2009). However, road mortality may be equal for adults and subadults: not only do subadults cross the road when dispersing, but both age classes also regularly cross to move from the park into the agricultural land. While individuals living exclusively within the park boundaries are not exposed to this threat and thus may have a higher survival rate, our data did not allow this distinction, because most of our studied individuals used both areas in and outside the park. Although we estimated apparent survival, and actual survival may be higher, a constant adult survival rate of 0.9 appears to be too high for this particular population and its long-term viability should be assessed accounting for adequate levels of temporal variation. Also, the survival rate for maned wolves living in entirely unprotected areas needs to be assessed separately, as in the present case, all individuals had a major refuge in ENP, which probably enhances survival.

Understanding population dynamics is important for conservation planning; yet, for many species of conservation concern, this information is still lacking. Here, we presented the first analytically sound estimates of maned wolf survival rates based on a long-term study. However, our dataset presents some drawbacks: the overall sample size is small, which may impair the accuracy of some of our estimates; resighting data were not collected in discrete time intervals, and as dead recovery only occurred within the study area, we estimated apparent rather than actual survival (Sandercock, 2006). Also, some tests of general model fit concerning a possible trap response could not be performed. Although we do not expect a behavioral response to 'resighting' by radio-telemetry, we cannot prove that our models fit the data adequately. A lack of fit can result in biased parameter estimates and underestimated standard errors (Pollock *et al.*, 1990). Thus, the survival rates presented here are tentative estimates. Still, they represent an important step toward a better understanding of the maned wolf's ecology and demonstrate the need for long-term studies that can yield crucial information for the species' conservation in the ever-changing Cerrado landscape.

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References

- Adams, L.G., Stephenson, R.O., Dale, B.W., Ahgook, R.T. & Demma, D.J. (2008). Population dynamics and harvest characteristics of wolves in the central Brooks Range, Alaska. *Wildl. Monogr.* **170**, 1–25.
- Beissinger, S.R. (2002). Population viability analysis: past, present, future. In *Population viability analysis*: 5–17. Beissinger, S.R. & McCullough, D.R. (Eds). Chicago: The University of Chicago Press.
- Boyce, M.S. (1992). Population viability analysis. *Annu. Rev. Ecol. Syst.* **23**, 481–506.
- Buckland, S.T., Burnham, K.P. & Augustin, N.H. (1997). Model selection: an integral part of inference. *Biometrics* **53**, 603–618.
- Burnham, K.P. (1993). A theory for combined analysis of ring recovery and recapture data. In *Marked individuals in the study of bird population*: 199–213. Lebreton, J.-D. & North, P.M. (Eds). Basel: Birkhauser Verlag.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer-Verlag.
- Cavalcanti, R.B. & Joly, C.A. (2002). Biodiversity and conservation priorities in the Cerrado region. In *The Cerrados of Brazil. Ecology and Natural History of a Neotropical Savannah*: 351–367. Oliveira, P.S. & Marquis, R.J. (Eds). New York: Columbia University Press.
- Ceballos, G., Erlich, P.R., Soberon, J., Salazar, I. & Fay, J.P. (2005). Global mammal conservation: What must we manage? *Science* **309**, 603–607.
- Chamberlain, M.J. (2001). Survival and cause-specific mortality of adult coyotes (*Canis latrans*) in central Mississippi. *Am. Midl. Nat.* **145**, 414–418.
- Choquet, R., Reboulet, A.M., Lebreton, J.D., Gimenez, O. & Pradel, R. (2005). U-CARE 2.2 User's Manual. CEFE, Montpellier, France. Available at <http://ftp.cefe.cnrs.fr/biom/Soft-CR/> (accessed 25 October 2009).
- Choquet, R., Reboulet, A.M., Lebreton, J.D., Gimenez, O. & Pradel, R. (2008). U-CARE V2.3. Available at <http://www.cefe.cnrs.fr/BIOM/en/software.htm> (accessed 25 October 2009).
- Dietz, J.M. (1984). Ecology and social organization of the maned wolf (*Chrysocyon brachyurus*). *Smiths. Contrib. Zool.* **392**, 1–51.
- Eisenberg, J.F. & Redford, K.H. (1999). *Mammals of the neotropics. Volume 3. The central neotropics: Ecuador, Peru, Bolivia, Brazil*. Chicago: University of Chicago Press.
- Gould, W.R. & Nichols, J.D.N. (1998). Estimation of temporal variability of survival in animal populations. *Ecology* **79**, 2531–2538.
- Hayes, R.D. & Harestad, A.S. (2000). Demography of a recovering wolf population in the Yukon. *Can. J. Zool.* **78**, 36–48.
- IBDF/FBCN. (1981). *Plano de Manejo do Parque Nacional das Emas (PNE)*. Brazil: Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis.
- IUCN. (2009). *IUCN Red List of Threatened Species. Version 2009.1*. Gland: IUCN. Available at <http://www.iucnredlist.org> (accessed 29 October 2009).
- Jácomo, A.T.A., Kashivakura, C.K., Ferro, C., Furtado, M.M., Astete, S.P., Tôrres, N.M., Sollmann, R. & Silveira, L. (2009). Maned wolf home-range and spatial organization in the Brazilian Grasslands. *J. Mammal.* **90**, 150–157.
- Jácomo, A.T.A., Silveira, L. & Diniz-Filho, J.A.F. (2004). Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. *J. Zool. (Lond.)* **262**, 99–106.
- Kamler, J.F. & Gipson, P.S. (2004). Survival and cause-specific mortality among furbearers in a protected area. *Am. Midl. Nat.* **151**, 27–34.
- Karanth, K.U. & Chellam, R. (2009). Carnivore conservation at the crossroads. *Oryx* **43**, 1–2.
- Karanth, K.U., Nichols, J.D., Kumar, N.S. & Hines, J.E. (2006). Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology* **87**, 2925–2937.
- Klink, C.A. & Machado, R.B. (2005). Conservation of the Brazilian Cerrado. *Conserv. Biol.* **19**, 707–713.
- Lambin, X., Aars, J. & Pieltney, S.B. (2001). Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. In *Dispersal*: 110–122. Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (Eds). New York: Oxford University Press.
- Lande, R. (2002). Incorporating Stochasticity in population Viability Analysis. In *Population viability analysis*: 18–40. Beissinger, S.R. & McCullough, D.R. (Eds). Chicago: The University of Chicago Press.
- Langguth, A. (1975). Ecology and evolution in the South American canids. In *The wild canids. Their systematics and behaviour*: 192–206. Fox, M.W. (Ed.). New York: Litton Educational Publishing.
- Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. *Ecol. Monogr.* **62**, 67–118.
- Marucco, F., Pletscher, D.H., Boitani, L., Schwartz, M.K., Pilgrim, K.L. & Lebreton, J.D. (2009). Wolf survival and population trend using non-invasive capture–recapture

- techniques in the Western Alps. *J. Appl. Ecol.* **46**, 1003–1010.
- Murray, D.L. & Patterson, B.R. (2006). Wildlife survival estimation: recent advances and future directions. *J. Wildl. Mgmt.* **70**, 1499–1503.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.
- Paula, R.C., Medici, P. & Morato, R.G. (Eds.). (2008). *Plano de Ação para a Conservação do Lobo-Guará. Análise de Viabilidade Populacional e de Hábitat (PHVA)*. Bras í lia: IBAMA.
- Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. (1990). Statistical inference for capture–recapture experiments. *Wildl. Monogr.* **107**, 1–97.
- Reid, J.M., Mills, L.S., Dunning, J.B. Jr, Menges, E.S., McKelvey, K.S., Frye, R., Beissinger, S.R., Anstett, M.-C. & Miller, P. (2002). Emerging issues in population viability analysis. *Conserv. Biol.* **16**, 7–19.
- Rodden, M., Rodrigues, F. & Bestelmeyer, S. (2004). Maned wolf *Chrysocyon brachyurus* (Illiger 1815). In *Status survey and conservation action plan. Canids: foxes, wolves, jackals and dogs*: 38–43. Zillero-Zubiri, C., Hoffmann, M. & Macdonald, D.W. (Eds). Available at <http://www.canids.org/cap/index.htm> (accessed 30 June 2006).
- Rodden, M., Rodrigues, F. & Bestelmeyer, S. (2008). *Chrysocyon brachyurus*. In *IUCN 2008. 2008 IUCN Red List of Threatened Species*. Gland: IUCN. Available at www.iucnredlist.org (accessed 4 April 2009).
- Rodrigues, F.H.G. (2002). *Biologia e conservação do lobo-guará na Estação Ecológica de Águas Emendadas, DF*. Ph.D. thesis, State University of Campinas, Campinas, Brazil.
- Sandercock, B.K. (2006). Estimation of demographic parameters from live encounter data: a summary review. *J. Wildl. Mgmt.* **70**, 1504–1520.
- Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Kataryia, V., Lamoreux, J., Rodrigues, A.S.L., Stuart, S.N., Temple, H.J., Baillie, J., Boitani, L., Lacher, T.E. Jr, Mittermeier, R.A., Smith, A.T., Absolon, D., Aguiar, J.M., Amori, G., Bakkour, N., Baldi, R., Berridge, R.J., Bielby, J., Black, P.A., Blanc, J.J., Brooks, T.M., Burton, J.A., Butynski, T.M., Catullo, G., Chapman, R., Cokeliss, Z., Collen, B., Conroy, J., Cooke, J.G., da Fonseca, G.A.B., Derocher, A.E., Dublin, H.T., Duckworth, J.W., Emmons, L., Emslie, R.H., Festa-Bianchet, M., Foster, M., Foster, S., Garshelis, D.L., Gates, C., Gimenez-Dixon, M., Gonzalez, S., Gonzalez-Maya, J.F., Good, T.C., Hammerson, G., Hammond, P.S., Happold, D., Happold, M., Hare, J., Harris, R.B., Hawkins, C.E., Haywood, M., Heaney, L.R., Hedges, S., Helgen, K.M., Hilton-Taylor, C., Hussain, S.A., Ishii, N., Jefferson, T.A., Jenkins, R.K.B., Johnston, C.H., Keith, M., Kingdon, J., Knox, D.H., Kovacs, K.M., Langhammer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L.F., Macavoy, Z., Mace, G.M., Mallon, D.P., Masi, M., McKnight, M.W., Medellín, R.A., Medici, P., Mills, G., Moehlman, P.D., Molur, S., Mora, A., Nowell, K., Oates, J.F., Olech, W., Oliver, W.R.L., Oprea, M., Patterson, B.D., Perrin, W.F., Polidoro, B.A., Pollock, C., Powel, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R.R., Reilly, S.B., Reynolds, J.E., Rondinini, C., Rosell-Ambal, R.G., Rulli, M., Rylands, A.B., Savini, S., Schank, C.J., Sechrest, W., Self-Sullivan, C., Shoemaker, A., Sillero-Zubiri, C., De Silva, N., Smith, D.E., Srinivasulu, C., Stephenson, P.J., van Strien, N., Talukdar, B.K., Taylor, B.L., Timmins, R., Tirira, D.G., Tognelli, M.F., Tsytulina, K., Veiga, L.M., Vié, J.-C., Williamson, E.A., Wyatt, S.A., Xie, Y. & Young, B.E. (2008). The status of the world's land and marine mammals: diversity, threat and knowledge. *Science* **322**, 225–230.
- Silveira, L., Furtado, M.M., Tôrres, N.M., Sollmann, R., Uhl, G. & Jácomo, A.T.A. (2009). Maned wolf density in a Central Brazilian Grassland Reserve. *J. Wildl. Mgmt.* **73**, 68–71.
- Trolle, M., Noss, A.J., Lima, E.S. & Dalponte, J. (2007). Camera-trap studies of maned wolf density in the Cerrado and the Pantanal of Brazil. *Biodivers. Conserv.* **16**, 1197–1204.
- Van Deelen, T.R. & Gosselink, T.E. (2006). Coyote survival in a row-crop agricultural landscape. *Can. J. Zool.* **84**, 1630–1636.
- White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46** (Suppl.), 120–138.