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IMPORTANCE OF ACCOUNTING FOR DETECTION HETEROGENEITY WHEN ESTIMATING ABUNDANCE: THE CASE OF FRENCH WOLVES

Sarah Cubaynes¹, Roger Pradel¹, Rémi Choquet¹, Christophe Duchamp², Jean-Michel Gaillard³, Jean-Dominique Lebreton¹, Eric Marboutin⁵, Christian Miquel⁴, Anne-Marie Reboulet¹, Carole Poillot⁴, Pierre Taberlet⁴, Olivier Gimenez¹

1. Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, campus CNRS, 1919 Route de Mende, F-34293 Montpellier Cedex 5.

2. Office National de la Chasse et de la Faune Sauvage, CNERA prédateurs et animaux déprédateurs, Parc Micropolis, F-05000 Gap.

3. Université de Lyon, F-69000, Lyon, Université Lyon 1, Centre National de la Recherche Scientifique, UMR 5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne.

4. Laboratoire d'Ecologie Alpine, UMR CNRS 5553, Université J. Fourier, BP 53, F-38041 Grenoble Cedex 9.

5. Office National de la Chasse et de la Faune Sauvage, ZI Mayencin, 5 allée de Béthléem, F-38610 Gières.

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Correspondence author:

Sarah Cubaynes

Centre d'Ecologie Fonctionnelle et Evolutive,
Unité Mixte de Recherche 5175, Campus CNRS,
1919 Route de Mende, 34293 Montpellier Cedex 5

France

Tel: +33 4 67 61 32 11

Fax: +33 4 67 41 21 38

E-mail: sarah.cubaynes@cefe.cnrs.fr

ABSTRACT

Assessing conservation strategies requires reliable estimates of abundance. As detecting all individuals is most often impossible in free-ranging populations, estimation procedures have to account for a less than one detection probability. Capture-recapture methods allow biologists to cope with this issue of detectability. However, capture-recapture models for open populations are built on the assumption that all individuals share the same detection probability, although detection heterogeneity among individuals has led to underestimating abundance of closed populations. We developed multievent capture-recapture models for an open population accounting for individual detection heterogeneity (IDH), and proposed an estimator of population size. We considered a two-class mixture model with ‘weakly’ and ‘highly’ detectable individuals to account for IDH. Using a non-invasive capture-recapture study of wolves based on genotypes identified in feces and hairs, we demonstrated that a strong underestimation of population size (27% on average) occurred when ignoring IDH.

Key words: *Canis lupus*, E-SURGE, mark-recapture, mixture models, multievent model, population size, individual heterogeneity.

INTRODUCTION

Assessing the success of conservation and management actions performed on focal populations relies on accurate estimates of population size. However, obtaining reliable abundance estimates is difficult for most taxa because exhaustive counting of free-ranging animals is most often impossible. Capture-recapture (CR) protocols have been developed to solve that problem, and are increasingly used to monitor populations of vertebrates (Williams et al. 2002).

In standard CR models, all individuals are assumed to have identical detection probabilities. However, individual attributes (e.g., age, body mass, social status) and habitat features (home range location and composition) generate heterogeneity in the detection process (IDH for *individual detection heterogeneity* hereafter) that has been shown to lead to biased estimates of abundance in closed populations (Carothers 1973; Gilbert 1973; Otis et al. 1978; Hwang & Huggins 2005) when it is ignored. In closed populations, IDH can be handled by considering classes of individuals with distinct detection probabilities using mixture models (Agresti 1994; Norris & Pollock 1996; Pledger 2000). Although some factors can be incorporated in CR models as individual covariates (Huggins 1989, 1994; McDonald & Amstrup 2001), most of them are generally not measured. Moreover, in the case of endangered and/or small-sized populations for which individuals are not physically captured but monitored through their DNA extracted from biological material collected in the field (e.g., Waits & Paetkau 2005), no covariate is available.

We sought to demonstrate the risks of flawed inference in the estimation of the size of open populations when IDH is ignored. We combined estimators of detection probabilities in heterogeneous open populations (Pledger et al. 2003) with an estimator of population size when individuals are sampled with unequal probabilities. We used multievent CR models (Pradel 2005, 2009) which allow considering hidden states, indirectly observed through the

observations. Here, we included two classes of individuals (i.e., highly vs. weakly detectable) to model IDH while estimating abundance.

To illustrate our approach, we used CR data on wolves (*Canis lupus*). After their extirpation from France two centuries ago, wolves entered the French Alps in 1992 as a consequence of the natural recovering process in adjacent Italy (Valière et al. 2003). Since then, the population has been increasing and individuals have spread across the Alps. Because of high extensive outdoor agricultural practices, a large number of depredations on livestock occurred, creating strong political and economical issues (Mech 1995). Reliable estimates of annual abundance are thus needed as the first step of a wolf action plan for population management as well as for evaluating the species conservation status in France. Large pack territories associated with low densities and high mobility prevented us using traditional surveys based on observations or physical recaptures. We used non-invasive monitoring via genotyping of biological material for individual identification of wolves (Taberlet & Luikart 1999). We applied models incorporating IDH to this individual monitoring, and evaluated the resulting bias in abundance when IDH was ignored. Eventually, we considered the benefits of accounting for IDH when estimating population size and how it could impact the reliability of conservation actions.

DATA AND METHODS

Data collection

We collected DNA samples from 1995 to 2003 in the French Alps using both an opportunistic sign survey at large scale and standardized snow-tracking field work within all pack territories. We developed microsatellite-based identification of wolves from scats to identify individuals (Valière et al. 2003). For each wolf sample, we amplified 7 microsatellite

loci using a PCR multi-tube approach with 8 replicates per sample (Taberlet & Luikart 1999). To assess the genotype reliability and minimize errors, we used a quality index (QI, corresponding to the mean frequency of the consensus genotype among the 8 replicates at each locus, Miquel et al. 2006). We discarded genotypes with average QI < 0.4. We constructed a ‘genetic capture history’ for each detected genotype by grouping the observations within 3-month periods from January 1. Overall, 1,181 wolf samples were genotyped among which 840 were classified as reliable. The number of detections varied from 1 to 91 depending on the genotype. The data set included the capture history of 160 different genotypes.

Multievent CR modeling

To account for IDH, we used mixture models (Pledger 2000; Pledger et al. 2003; Pradel 2009) that incorporate hidden groups of individuals with contrasting detection probability. We did not have a priori information on the detection rate for any genotyped wolf. Thus our model looked like a usual CR model in which the state of each individual was imperfectly known, and therefore described a particular case of multi-event CR models that specifically deal with uncertainty in state assignment (Pradel 2005).

A multievent CR model includes both states and observations which are generated from the underlying state of an individual. We distinguished wolves alive with high detection probability (‘H’), wolves alive with low detection probability (‘L’), and dead wolves (‘D’). The observations were coded ‘0’ (when a previously genotyped wolf was not detected) and ‘1’ (when it was detected). For example, the capture history ‘101’ denotes an individual who was encountered on the first and third sampling occasions, but missed on the second. The probability of this history is:

$$\text{Pr}(101) = \pi \cdot \phi \cdot (1 - p^L) \cdot \phi \cdot p^L + (1 - \pi) \cdot \phi \cdot (1 - p^H) \cdot \phi \cdot p^H$$

where π is the probability that the individual belongs to state L, p^L and p^H are the recapture probabilities in states L and H, and ϕ is the common survival probability. Assuming all individuals have equal detection probability (homogeneity model), we get the standard Cormack-Jolly-Seber model (Lebreton et al. 1992). We also tested for differences in survival of wolves between states L and H (Supplementary Material), as detection rate might be related to the social status.

We then defined a set of candidate models incorporating biologically relevant combinations of several temporal and individual effects on both survival and detection probabilities. Regarding temporal effects, we considered ‘year effect’ to test for the influence of poaching or some years of high juvenile mortality and ‘seasonal effect’ to explore climate impact on survival. To investigate temporal variations in sampling effort we considered year and seasonal effects on detection. Moreover, regarding detection, we divided the year in two ways. First, we expected detection to remain lower for some time after reproduction (July to December) because the cubs, and to some extent the pack itself, are relatively sedentary (‘biology effect’ hereafter). Second, we expected a higher detection probability in the ‘cold’ period (October to March), as cold and snow are favorable to DNA conservation (‘climate effect’ hereafter) (Lucchini et al. 2002).

To choose among models and assess the effect of detection heterogeneity on abundance estimation, we selected the model with lowest AICc (Burnham & Anderson 2002). We used program E-SURGE (Choquet et al. 2009) to perform CR analyses (Appendix S1). Although goodness-of-fit tests are well developed for standard open CR models (Lebreton et al. 1992), there is no test available for multievent CR models (Pradel 2009). However, an ad-hoc procedure was recently proposed to test the goodness-of-fit of a model with heterogeneity in detection probabilities (Péron et al. unpubl. data). Using program U-CARE (Choquet et al. 2005), we rejected the CJS model ($X_{115}^2 = 180.73, p < 0.01$), but the corresponding model

accounting for detection heterogeneity fitted the data appropriately ($X_{113}^2 = 118.996$, $p = 0.331$). Consequently, all candidate models accounted for IDH.

Population size estimation

In a model with homogeneous detection probabilities, the number of individuals N_t alive at time t is estimated from the ratio of the number captured n_t over an estimate \hat{p}_t of the detection probability at time t , $\hat{N}_t = \frac{n_t}{\hat{p}_t}$. The sample n consists of u newly detected individuals and m previously detected. In the same way, N_t consists of the sum of U_t new individuals and M_t individuals already present and still alive at time t . In the heterogeneity model, the newly detected are made of $\pi \cdot U_t$ individuals in state L and $(1 - \pi) \cdot U_t$ individuals in state H. Using a Horvitz-Thompson type estimator which specifically accounts for unequal detection probabilities, we obtained an estimate \hat{U}_t of the expected number of new individuals in the population

$$\hat{U}_t = \frac{\hat{\pi} \cdot u_t}{\hat{p}_t^L} + \frac{(1 - \hat{\pi}) \cdot u_t}{\hat{p}_t^H} .$$

Applying the survival estimates to already detected individuals, we obtained an estimate \hat{M}_t of the expected number of already detected individuals still alive at time t

$$\hat{M}_t = \sum_{j=1}^{t-1} u_j \cdot \left(\hat{\pi} \cdot \prod_{i=1}^{t-1} \hat{\phi}_i^L + (1 - \hat{\pi}) \cdot \prod_{i=1}^{t-1} \hat{\phi}_i^H \right) .$$

Finally, we obtained an estimator of population size accounting for IDH (Appendix S1)

$$\hat{N}_{het,t} = \hat{U}_t + \hat{M}_t .$$

For example, let us consider a population with $\hat{\pi} = 30\%$ of individuals in state L, $\hat{p}_t^L = 0.2$ and $\hat{\phi}^L = 0.6$ and with $1 - \hat{\pi} = 70\%$ of individuals in state H with $\hat{p}^H = 0.5$ and $\hat{\phi}^H = 0.9$. If

$u_1 = 1$ individual is newly detected at the first occasion and $u_2 = 2$ at the second occasion,

$$\hat{U}_2 = \frac{0.3 \times 2}{0.2} + \frac{0.7 \times 2}{0.5} = 5.8 \text{ and } \hat{M}_2 = 1 \times (0.3 \times 0.6 + 0.7 \times 0.9) = 0.81, \text{ we obtain an estimate}$$

of the size of the population at the second occasion $\hat{N}_{het_2} = 5.8 + 0.81 = 6.61$.

Given the discrete and positive nature of the data, and the relatively small sample size, we used a non-parametric bootstrap (Davison & Hinkley 1997) to obtain confidence intervals of abundance and functions of demographic parameters.

RESULTS

The model with individual heterogeneity in both detection and survival probabilities was best supported by the data (Appendix S2). Temporal variation in survival received little support from the data and did not affect detection parameters estimates (results not shown). We therefore retained models with constant survival only. Detection probabilities exhibited a semester effect acting on an additive scale with heterogeneity. In support to the goodness-of-fit tests, models with a two-class mixture on detection always had lower AICc values than their homogenous counterpart (Appendix S2). Although there was some uncertainty on whether heterogeneity should also be incorporated on survival, detection parameters estimates given by the four top models were very similar.

The detection probability was higher from January to June than from July to December in both L and H states (Table 1). Detection probability strongly differed in the two classes of detectability. Depending on which of the two 6-month periods we considered, the detection probability of wolves in state H was 4-6 times greater than that of wolves in state L. Annual survival (product of all 3-month survival probabilities) of wolves in state H was 90% (95% CI: [0.71; 0.98]) versus 75% (95% CI: [0.54; 0.94]) for wolves in state L. Overall, our

results suggested a positive correlation between survival and detection probabilities, with weakly (resp. highly) detectable individuals having a low (resp. high) survival probability.

[Table 1 about here]

The total population size of wolves in the French Alps increased from 3 (95% CI: [0;7]) in winter 1995 to 126 (95% CI: [85; 280]) in winter 2003 (Figure 1). Marked seasonal variations were observed, with peaks after the breeding season, and decreasing periods that were synchronized with dispersal events. When IDH was ignored (Figure 1), abundance was underestimated by 27% on average (ranging from 0% to 70%).

[Figure 1 about here]

DISCUSSION

Wolf populations are increasing in Europe (Salvatori & Linnell 2005) which often translates into increasing conflicts due to depredation on livestock. Although large carnivores are protected by law (Bern Convention, European Fauna-Flora-Habitat Directive), the long term persistence and reestablishment of populations is based on their acceptance by the different stakeholders (Bath 2000). To this aim, if the conservation status of the species is favorable, governments may implement management strategies involving some form of lethal control (Treves & Karanth 2003). Assessing a sustainable level for lethal control requires a reliable estimate of abundance, which may be hampered if IDH is ignored. Both goodness-of-fit tests and model selection procedures indicated that IDH occurred among wolves. Detection heterogeneity could result from genotyping errors (Lukacs & Burnham 2005), heterogeneities in the sampling effort (Devineau et al. 2006) or be a direct

consequence of the species biology (Crespin et al. 2008). We used multi-tube PCR and discarded unreliable genotypes to minimize errors. Among reliable samples, genotypes detected only once did not have a lower QI than genotypes detected more than once ($X_1^2 = 1.854$ $p = 0.17$), showing no evidence for false genotypes.

To disentangle the effects of sampling heterogeneity from the species biology, we compared between periods within the year. The ‘biology’ effect was more plausible than the ‘climate’ effect, with detectability higher before than after the breeding period. The lower detection probability after the breeding period may reflect the impossibility to detect cubs before 6 months when they start to follow adults. Under this scenario, ‘highly detected individuals’ would correspond to dominant individuals that are more mobile on the pack territory and more keen on using feces or urine to mark the territory (Vila et al. 1994), whereas ‘weakly detectable individuals’ would be made of young and subordinates that are supposed to be hardly detectable because of a lack of mobility or a life passed outside the pack territory (Mech & Boitani 2003). This is reinforced by the estimated survival of ‘highly detectable individuals’ which matches the survival of dominant individuals reported in other studies (Mech & Boitani 2003). The lower survival of ‘weakly detectable individuals’ could be attributed to a mixture of cubs, subordinates and migrants which have a lower survival than dominant individuals. However, the model specifying a transition of individuals from the class of ‘lowly’ to ‘highly’ detectable – allowing subordinate individuals to access the dominant status – was not supported by the data ($\Delta AICc = -56.29$ when compared with a model without transition). The limited length of the study period combined with a small dataset may be insufficient to detect transitions.

Link (2003) has established that the same capture history data set may arise from a wide range of heterogeneity models, which in turn yield entirely different estimates of population size. Based on biological considerations and following Pledger et al. (2000)’s

suggestion, we used a simple dichotomy of individuals (i.e., low versus high detection). Note, moreover, that the limited size of our dataset prevented us using a larger number of classes.

Problems of non-identifiability of population size may also arise when some individuals have encounter probabilities close to zero (Link 2003). In wolves, the chance of detection of subordinates is not very low and probably similar among them because packs occupy a territory and, especially in winter, it is possible to follow the tracks and find the droppings of all individuals along the way. The really problematic individuals are the dispersing individuals which do not belong to a pack. They are probably secretive, do not stay very long in the same area, and may escape detection entirely. Because of them, our estimate of population size is likely to be biased low. However, we believe that our estimate remains useful because the dispersers represent a minority of individuals and they eventually join a pack and become detectable or they leave the study area entirely (or die).

We demonstrated that ignoring IDH can lead to a severe underestimation of population size and proposed a procedure based on multi-event CR methods to account for IDH in free-ranging populations.

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SUPPLEMENTARY MATERIAL

Appendix S1 and Appendix S2 are available as part of the on-line article from <http://www.blackwell-synergy.com/>. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

TABLE LEGEND

Table 1. Parameter estimates and 95% confidence intervals (in parentheses) of the best-fitting model assuming a two-class mixture of individuals on survival and detection probabilities, with an additive 6-month period effect on the later. Note: The detection probability over a semester was calculated as the probability of being detected at least once during this period, e.g. the detection probability over January- June was equal to the detection probability over January-March plus the detection probability over April-June minus the detection probability over January-March times the detection probability over April-June.

TABLE 1

Parameter	Class of individuals	
	Weakly detectable	Highly detectable
Proportion of newly marked individuals	0.76 (0.65;0.85)	0.24 (0.15;0.34)
Survival probability	0.75 (0.54;0.94)	0.90 (0.71;0.98)
Detection probability over January- June	0.22 (0.11;0.37)	0.86 (0.74; 0.96)
Detection probability over July- December	0.10 (0.05;0.18)	0.64 (0.51;0.82)

FIGURE LEGENDS

Figure 1. Population size estimates of wolves in the French Alps from 1995 to 2003. Results were obtained from the best-fitting model assuming a two-class mixture of individuals on survival and detection probabilities, with a semester effect on the later (*solid line*) and a model with a similar structure but ignoring individual heterogeneity in the detection (*dashed line*). A non-parametric bootstrap procedure was used to obtain 95% confidence intervals (vertical bars).

FIGURE 1

