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ORIGINAL PAPER

Assessment of methods for estimating wild rabbit population abundance in agricultural landscapes

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Abstract Various methods have been used to estimate rabbit abundance, but comparisons of standard methods are still lacking, and thus, results remain roughly comparable across studies. Ideally, a method should be applicable over a wide range of situations, such as differing abundances or habitat types. Comparisons of methods are required to evaluate the benefits of each of them, and survey methods should be validated for the conditions in which they will be used. In this study, we compare the performance of direct methods (kilometric abundance index and distance sampling) in two seasons and at two times of day (dusk and night) for estimating wild rabbit abundances in agricultural landscapes. Estimates based on direct methods were highly correlated and detected similar seasonal population changes. Night counts provided better estimates than did dusk counts and exhibited more precision. Results are discussed within the context of rabbit behaviour and their implications for rabbit population surveys.

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Introduction

Estimates of the size of wildlife populations are fundamental to many aspects of conservation biology and wildlife management, e.g. setting conservation priorities or developing management programmes (Thomas et al. 2006; Newson et al. 2008). Calculations of true population sizes are often prohibitively expensive, but several survey methods have been developed to estimate population size or the relative abundance of species (Tellería 1986). The suitability of a method can depend on a variety of factors, including the specific management questions being addressed, the degree of precision required and the costs involved (Thomas et al. 2006). A single best method for estimating animal abundance is unlikely to apply in all circumstances; therefore, sampling methods have to be individually designed for or adapted to the particular needs of each population (Langbein et al. 1999).

European rabbits (*Oryctolagus cuniculus*) are considered a pest in several regions of the world; e.g. Australia, New Zealand and Great Britain, because they damage crops and forest stands, among others. Within their native range on the Iberian Peninsula, rabbit populations have suffered a sharp decline in recent decades and, currently (2009), are at low densities throughout the region (Delibes-Mateos et al. 2009). In some areas, however, local rabbit populations have recovered and reach high densities. Most of those areas are agricultural landscapes that have soft soils, where it is easier for rabbits to build warrens (Calvete et al. 2004; Williams et al. 2007) and where rabbits are an important game species (Delibes-Mateos et al. 2008). Accurate estimates of rabbit

numbers are useful in predicting the economic costs of rabbit damage and in gauging the effectiveness of methods of population control (Poole 2003).

The techniques used to assess rabbit population sizes include indirect methods, in which signs of rabbit activity are used to estimate rabbit abundance, and direct methods, such as trapping or counts of individuals observed. Indirect methods are particularly useful for nocturnal or elusive species such as rabbits (Poole 2003), and they are often the only practical means of quantifying levels of habitat use when direct sampling is difficult. However, few studies have tried to compare the results of indirect vs. direct methods (Palomares 2001; Ballinger and Morgan 2002), and their validity remains questionable. On the other hand, direct methods provide a rapid, simple means of assessing rabbit abundance, which makes sampling over large areas feasible (Williams et al. 1995); however, differences in detectability among habitats and species behaviour can undermine the suitability of direct methods.

Crude population indices such as the kilometric abundance index (KAI), i.e. the number of individuals observed per kilometre, have been used widely to quantify rabbit abundance and population trends in Spain (Beltrán 1991; Moreno et al. 2007; Williams et al. 2007) and France (Marchandeau and Gaudin 1994). KAIs have been successful in estimating the sizes of other vertebrate populations across a wide range of densities, which allowed comparisons between localities that had similar habitat structure (Acevedo et al. 2008). Although KAIs show a good reproducibility (Marchandeau and Gaudin 1994), their use is quite controversial, and their validity has been questioned (Engeman 2005). Criticisms involve variation in the detectability of animals spatially and temporally because KAIs do not control for habitat permeability (Marchandeau et al. 2006; Thomas et al. 2006). In contrast, distance sampling methods take into account variation in visibility: The number of objects detected is modelled as a function of the perpendicular distance from the transect line (Thomas et al. 2006). Distance sampling is used widely to estimate the relative abundances of animal species (Ruette et al. 2003; Newson et al. 2008), from whales to terrestrial vertebrates. It has been used to estimate the population densities of other lagomorphs, i.e. hares (Newey et al. 2003; Reid and Montgomery 2007), and has been proposed as a practical means of estimating their abundance at the regional scale (Langbein et al. 1999). Despite its potential advantages, distance sampling has seldom been applied to rabbits (but see Blanco and Villafuerte 1993; Palomares 2001; Martins et al. 2003; Moreno et al. 2007), and its accuracy for this species has not been compared with other standard methods of assessing rabbit populations before.

Direct methods based on counts of individuals depend on the probability of detection of animals, which is influenced by several factors, such as observer-related, environmental, and species-specific factors (Thomas et al. 2006). For instance, animal behaviour can influence significantly the accuracy and precision of density estimates derived from distance sampling (Ward et al. 2004; Hounsome et al. 2005). Rabbits are crepuscular–nocturnal, and their activity follows circadian rhythms; thus, the timing of the census can significantly affect the results (Ballinger and Morgan 2002). To estimate rabbit abundance, direct methods based on dusk or night counts are indistinctly used, and their results are confounded in the literature. Night counts have been widely applied to monitor rabbit populations (Marchandeau and Gaudin 1994; Martins et al. 2003; Marchandeau et al. 2006) and to estimate population trends (Caley and Morley 2002; Williams et al. 2007), and they have shown to be reliable population indices when compared to capture–mark–recapture methods (Ballinger and Morgan 2002). On the other hand, dusk counts have been also used (Blanco and Villafuerte 1993; Palomares 2001; Martins et al. 2003; Moreno et al. 2007) and even proposed as the best method to estimate rabbit populations in the Mediterranean region (Blanco and Villafuerte 1993). A comparison of the abundance indices obtained before and after dusk might help to improve the accuracy of the population density estimates of rabbits within their native range in Spain.

The objectives of this study were to compare the performances of different estimates of rabbit populations based on direct methods, i.e. distance sampling and KAIs, across a range of time periods (dusk vs. night counts) and seasons under a range of agricultural conditions.

Material and methods

Study area

The study was conducted in an agricultural area within Córdoba province, southern Spain, which has a dry Mediterranean climate and calcareous soils. Traditionally, those agricultural lands have been devoted to olive groves, vineyards and cereals (García-Montoya 1989). Today, small-game hunting is important in the area, and rabbits occur in large numbers.

Sampling methods Seven transects approximately 10-km long were established along dirt tracks at random within the study area. Rabbits were counted along transects from a vehicle travelling approximately 10 km/h. Each survey occurred on three consecutive days, in clear weather conditions, and avoided days when hunting was permitted. Surveys were conducted by a driver and another observer inside the vehicle, 1 h before dusk (hereafter, dusk counts)

and repeated 1 h after sunset with the observer standing upright through a sunroof, scanning the fields with a 100-W handheld spotlight (hereafter, night counts). To avoid observer bias, the same experienced observer (ICB) conducted all of the surveys. Enough time (about 2 h) was allowed between the dusk and night counts to ensure the independence of the counts and minimise the disturbance to the animals (Martins et al. 2003). In both cases, the distance from the observer to a rabbit was measured using a Leica rangefinder (LRF 1200 Scan, Solms, Germany; range= 15–1,100 m, precision ±1 m/±0.1%), and compass bearings were recorded to determine the angle between the line transect and the animal or group of animals observed (clusters). Surveys were performed in October 2007 and June 2008, which coincided with the times of the year of the minimum and maximum annual rabbit abundances in Mediterranean areas, respectively (Moreno et al. 2007).

For each transect, season, and type of count (dusk or night counts), we calculated a crude index of rabbit abundance, the KAI, by averaging the number of rabbits counted per kilometre. Distance Sampling 5.0 software (Thomas et al. 2006) was used to estimate rabbit density. Six commonly used models and adjustment terms were constructed (Thomas et al. 2006), including uniform cosine, uniform simple polynomial, half-normal cosine, half-normal hermite polynomial, hazard rate cosine, and hazard rate simple polynomial. The best model was the model that had the lowest value of Akaike's Information Criterion. To calculate rabbit density, a hazard-rate function with a cosine series expansion was fitted to the data, which were truncated at 145 m, and sightings within the first 25 m were pooled.

To enable comparisons between distance sampling estimates and KAIs and to avoid pseudoreplication, distance-sampling estimates and KAIs were obtained on different days within the same locality (Acevedo et al. 2008). First, we assessed the relationship between the methods using those independent data sets. Second, because the independence of distance-sampling estimates and KAIs was confirmed, we used all of the data to calculate the two abundance indices.

To compare the performance of direct methods and assess the effect of time of day and season on the estimates, linear mixed models were used, considering transect as a random factor in all models. Thus, four models were built, considering distance-sampling and KAI estimates and their coefficients of variation as dependent variables, respectively. Season, time of day and the interaction term between season and time were considered as fixed-effect independent variables. One additional model was built to assess the relationship between distance sampling and KAI estimates, for independent data sets and all data. Statistical analyses were performed using R 2.8.1 (R Development Core Team 2008).

Results

General results

During surveys, 3,005 rabbits were observed in 1,973 clusters. Distance sampling and KAI estimates were significantly higher for night counts than for dusk counts (Fig. 1). With both methods, results were higher in June than they were in October. The distance-sampling and KAIs did not find a significant interaction between season and time in predicting density estimates (Table 1). Coefficients of variation of distance-sampling estimates ranged between 3.98% and 48.25% and were significantly lower in the night counts (mean CV night=11.11%) than in the dusk counts, but no significant seasonal differences were apparent. Coefficients of variation of the KAI estimates ranged between 4.33% and 110.75% and were significantly lower in the night counts (mean CV night=21.07%) than in the dusk counts, but again, no significant seasonal differences were apparent (Fig. 1).

Comparison of methods

The estimates of relative rabbit abundance derived from distance sampling and KAIs were significantly and positively correlated when the estimates were based on independent data sets or when all of the data were included (Table 1).

Discussion

In an agricultural area in southern Spain, night counts were better than dusk counts in estimating wild rabbit densities. Rabbits are most active at twilight and night (Blanco and Villafuerte 1993), but there is no consensus on when to conduct rabbit counts in Spain. Some have relied on dusk counts (Blanco and Villafuerte 1993; Moreno et al. 2007), while others used night counts (Gortázar 1997; Williams et al. 2007), making their results roughly comparable. In a study in SW Spain, Villafuerte et al. (1993) concluded that dusk was the best time to conduct rabbit censuses because activity at that time of day was the least dependent on environmental factors. In contrast, we found that night counts performed in clear weather conditions consistently registered larger numbers of rabbits than censuses performed at dusk and were less variable both across seasons and successive counts. This can be explained because their night counts refer to midnight, when rabbits are less active above ground than they are earlier at night (Ballinger and Morgan 2002). In addition, the proportion of animals above ground in our study appeared to be the same at both times of year, as suggested by the lack of interaction between

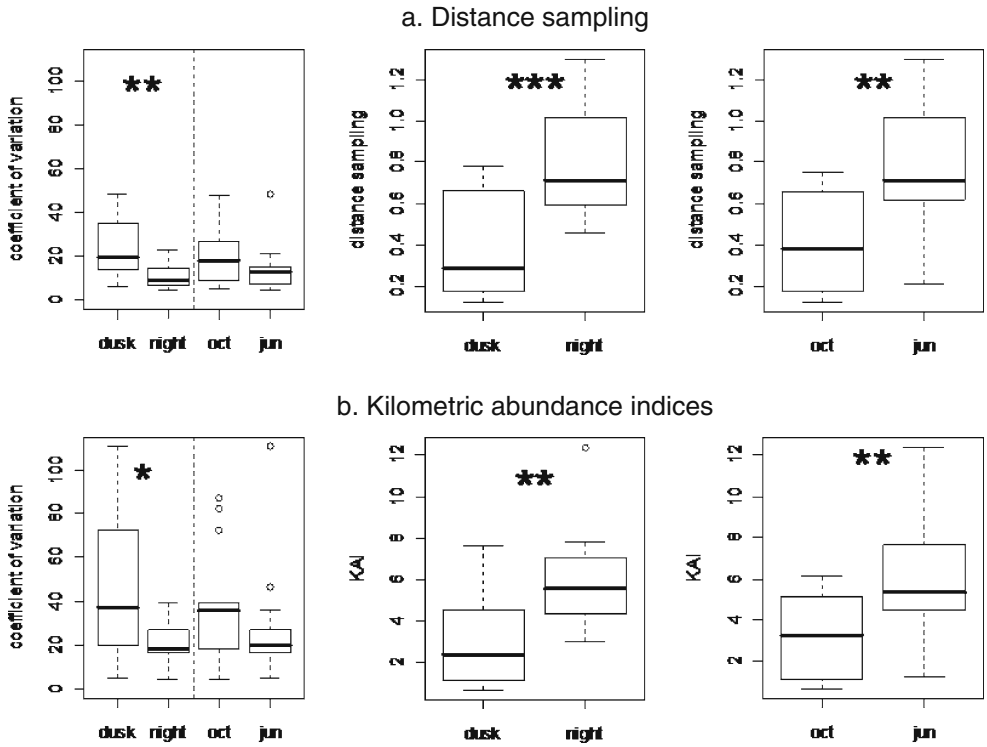

Fig. 1 Population estimates and coefficients of variation in rabbit populations in southern Spain derived using distance sampling (**a**) and kilometric abundance index (**b**) and based on dusk and night counts at two times of the year (October and June). *$p<0.05$; **$p<0.01$; ***$p<0.001$

season and time in predicting density estimates. Similarly, Ballinger and Morgan (2002) found that time of year had a minor effect on the emergence rates of rabbits from burrows. However, a seasonal variation has been reported in Mediterranean environments (Martins et al. 2003). They hypothesised that, in these areas, foraging activities might be extended throughout the daylight hours during the post-breeding period (July to September), coinciding with the

Table 1 Linear mixed models results for the direct methods estimates, coefficients of variation and the comparison between methods

	F	*df*	*p* value	*F*	*df*	*p* value
Direct methods estimates						
	Dependent variable: distance			Dependent variable: KAI		
	Random factor: Transect			Random factor: Transect		
Intercept	295.657	1,18	0.000	145.171	1,18	0.000
Season	26.982	1,18	0.001	14.274	1,18	0.001
Time	32.197	1,18	0.000	16.893	1,18	0.001
Season × time	0.215	1,18	0.648	0.844	1,18	0.370
Coefficients of variation						
	Dependent variable: CV distance			Dependent variable: CV KAI		
	Random factor: Transect			Random factor: Transect		
Intercept	46.713	1,18	0.000	49.056	1,18	0.000
Season	2.843	1,18	0.109	1.209	1,18	0.286
Time	11.354	1,18	0.003	6.956	1,18	0.017
Season × Time	0.197	1,18	0.662	0.396	1,18	0.537
Comparison between methods						
	Dependent variable: distance			Dependent variable: distance		
	Random factor: Transect			Random factor: Transect		
	Independent data			All data		
Intercept	209.110	1,26	0.000	601.092	1,26	0.000
KAI	37.581	1,26	0.000	190.748	1,26	0.000

depletion of food resources and a seasonal increase in the size of populations. In contrast, longer nights in winter make daylight emergence unnecessary, and therefore, higher numbers of rabbits are expected to be seen at night in winter and the breeding season (Martins et al. 2003). However, other factors shaping local activity patterns, such as antipredatory strategies (Blanco and Villafuerte 1993) or disturbance (Poole 2003), might be masking this seasonal variation in our study. For instance, human disturbance and hunting activity during the day, coupled with the occurrence of few nocturnal carnivores in our study area, may be determining the consistent trend observed.

Distance sampling and KAIs produced similar estimates of rabbit densities and detected seasonal changes similarly. In addition, the two methods indicated high precision (low CV) in the night counts, which indicates strong reproducibility (Marchandeau and Gaudin 1994). Thus, both methods were equally suited to estimate rabbit population trends in our study area, and the choice of a method would depend on the particular aims of the survey, as well as on the economic and logistic constraints. If a rough estimate of abundance is required or the objective is to monitor changes, KAIs might suffice. Distance sampling is a reliable means of comparing localities that differ in habitat structure, but it requires considerable sampling effort, and the underlying assumptions must be met (Acevedo et al. 2008).

Not all sampling designs, however, can meet the assumptions of the distance sampling method, which assumes that all animals on (or near) the transect line are always detected. Often, that assumption is problematic for surveys of cryptic and mobile species, or where habitat structure prevents the animals from being seen, even if they are present (e.g. in burrows; Hounsome et al. 2005). Thus, rabbit emergence behaviour is critical in spotlight counting because only rabbits that have emerged from burrows can be detected (Marchandeau et al. 2006). Indeed, just after dark, about 60% of the population of rabbits are aboveground simultaneously (Ballinger and Morgan 2002; Poole 2003). If it is suspected that a proportion of the population is not available for sampling on the line transect, as is the case, an independent method such as radio tracking should be incorporated into the design of the survey, which can improve the accuracy of estimates. In any case, to maximise the number of animals that can be detected in surveys of species that use warrens, data on behaviour and local activity patterns in the study area should be obtained.

The estimates derived from KAIs in our study areas were similar to those obtained in other Mediterranean areas before the outbreak of rabbit haemorrhagic disease [seven rabbits per kilometre (Moreno et al. 2007); eight rabbits per kilometre (Beltrán 1991)] but were much lower than those found in places where rabbits were introduced, e.g. Australia [25 rabbits per kilometre (Ballinger and Morgan 2002)] and New Zealand [125 rabbits per kilometre (Fletcher et al. 1999)]. Although the European rabbit is a well-known coloniser where it has been introduced, rabbit populations have declined dramatically within the species' native range (Lees and Bell 2008). In our study area, rabbit populations were at medium to high densities and appeared to be recovering, at least in sites that had favourable habitat and rabbit management strategies (Williams et al. 2007).

Implications for rabbit surveys

In our study, rabbit behaviour had a significant effect on abundance estimates, and we suggest that a pilot study should be conducted before the survey to identify local patterns of rabbit activity. In our study, night counts performed better and showed higher precision than dusk counts. In agricultural landscapes like ours, both distance sampling or kilometric abundance indices can be used, depending on the aims of study: KAIs are appropriate when relative abundance or population trends are required, and distance sampling should be used to estimate densities.

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