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Assessing the effects of a highway on a threatened species using Before–During–After and Before–During–After-Control–Impact designs

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ABSTRACT

Due to the growing awareness of potential impacts of roads, managers demand well-designed studies about the implications of linear infrastructures on ecosystems. We illustrate the application of Before–During–After and Before–During–After-Control–Impact designs (BDA and BDACI) to assess effects of highway construction and operation using a population of great bustards (*Otis tarda*) as a model. Based on a time series of demographic and distribution data (1997–2009), we developed generalized additive models and classification trees to test the effect of road distance on bustard distribution, identify road-effect distances and explore the seasonality of these effects. Two control zones were selected to test the changes between construction phases on productivity, and population trends using TRIM models. From the start of the road construction, great bustards tended to avoid close proximity to the highway (ca. 560–750 m threshold distance). The exclusion band was narrower during the breeding season. In addition, family groups were less tolerant to highway operation disturbances, as shown by their higher distance effect (ca. 1300 m). Population trends did not differ between impact and control zones during the construction. However, once the highway was in operation, bustard numbers declined gradually up to 50% in the impact zone, remained stable in the closest control zone, and increased in the zone located at the greatest distance from the highway. The effects on density of family groups were less evident. Our approach provides information relevant to great bustard conservation and suggests methods for obtaining information of interest to road managers, that could be applied to linear infrastructures with others species.

1. Introduction

Population growth and increasing demands for connectivity among human settlements have created a huge transport network, with a total length of current roads exceeding 69 million km worldwide (CIA, 2009). Roads are recognized as pervasive vectors of landscape change (Forman et al., 2003), and their impacts on wildlife are a major concern for managers, who are in need of reliable information to support their conservation decisions (e.g., Ament et al., 2008). As a consequence, the study of road effects on biological diversity and ecological processes has grown recently (e.g., Balkenhol and Waits, 2009; Coffin, 2007; Fahrig and Rytwinski, 2009), creating a new scientific discipline called road ecology (Forman, 1998).

Roads usually have profound edge and road-zone effects on habitat quality (Forman and Deblinger, 2000; Reijnen et al., 1996). Even though not all species are equally affected by roads, their presence usually implies some degree of habitat fragmentation (Jaeger et al., 2007), with short or long-term changes in spatial distribution (Pruett et al., 2009) and demographic structure (Tanner and Perry, 2007) of wildlife populations. These changes may eventually affect their genetic diversity and viability (Clark et al., 2009; Epps et al., 2005).

Several methods have been suggested to detect impact of human infrastructures or activities on the environment and on wildlife populations (e.g., Green, 1979; Stewart-Oaten et al., 1986; Wiens and Parker, 1995). One of the most powerful tools is the Before–After-Control–Impact (BACI) design, which uses sampling at control and impact zones through time to provide replication within the "before" and "after" periods (Stewart-Oaten et al., 1986). This approach is widely used in the environmental monitoring literature, to evaluate impacts of temporal activities (e.g., diving: Claudet et al., 2010; hunting: Czetwertynski et al., 2007) or permanent structures (e.g., wind farms: De Lucas et al., 2005; hydroelectric reservoirs: Nellemann et al., 2003), as well as to estimate ecological outcomes of habitat restoration (e.g., Geraldi et al., 2009; Pabian and Brittingham, 2007). BACI design can be applied to a high diversity of organisms, and enables the exploration of a variety of responses, such as changes in abundance, diversity, biomass or body condition. Compared to Control–Impact (CI) or Before–After (BA), the BACI design reduces the effects of temporal and spatial variation by subtracting

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out naturally varying temporal effects. This is a key advantage, as one of the main practical problems of detecting human influence on population abundances is the large temporal variance of many populations (Underwood, 1994).

Despite the potential power and usefulness of BACI designs there are very few published examples for roads (e.g., Chen et al., 2009; Hedrick et al., 2010), because of the need for repetitive sampling over a long period of time, which is expensive and difficult to achieve. Since long-term data series are usually missing, studies typically compare numbers and distributions of the species between impact and control areas once the road causing the impact has been constructed. This method, albeit useful in revealing important information, has important weaknesses that may bring into question the strength of the results (Fahrig and Rytwinski, 2009). Therefore, there remains an urgent need for well-designed studies of road effects on wildlife populations, which can be used to support decision-making during infrastructure planning (Benítez-López et al., 2010; Fahrig and Rytwinski, 2009; Roedenbeck et al., 2007). We used Before–During–After and Before–During–After-Control–Impact designs (BDA and BDACI; Roedenbeck et al., 2007), which also consider potential effects during infrastructure construction. Monitoring populations through the construction period increases our knowledge about effects occurring specifically during this phase, and disappearing once the infrastructure is completed, e.g., effects caused by earthworks, noise or other disturbances caused by trucks.

The primary aim of this study was to apply BACI designs to detect and assess the effects of highway construction on wildlife. As a model species we used the great bustard *Otis tarda*, a globally threatened steppe bird inhabiting farmland habitats and suffering severe population declines in recent decades partly due to infrastructure development (IUCN, 2010). Agro-steppes host many other endangered species that have been affected by both agricultural intensification and infrastructure expansion (Sanderson et al., 2002; Wretenberg et al., 2007). Steppe birds are indeed at present the most threatened bird group, with 83% of the species subject to unfavorable status (BirdLife International, 2004; Donald et al., 2006). Therefore, understanding the response of steppe wildlife to road construction may facilitate conservation decisions, an issue of growing concern for managers (Santos and Suárez, 2005). Our previous records on numbers and distribution of great bustards in the study area represent a unique opportunity to examine road impacts, since the possibility of assessing populations prior, during and after road development is rare. Specifically, we focused our research on two classical road effects. (1) Changes in the spatial distribution of bustard flocks. We determined road-effect distances through the identification of threshold distances to the highway indicating changes in bird abundance. We also assessed the seasonality of road-effect distances and the differences in avoidance behaviour of flocks and families. (2) Changes in population dynamics in areas near the highway. We tested whether highway construction induced changes in population trends and productivity in impact and control areas. The demographic and spatial data were collected during three time periods (13 years) at three zones. Our results indicate solid evidence for behavioural changes in a bird species due to a new road. In addition, this research provides relevant information and useful recommendations for the impact assessment of road developments, as well as for the management of the species studied.

2. Materials and methods

2.1. Study species

The great bustard is one of the heaviest flying birds (Alonso et al., 2009). It is adapted to pseudo-steppes of cereal farmland, which currently constitute its main habitat in Europe through its whole distribution range, from the Iberian Peninsula to China. Spain is home to 60–70% of this species' world population (Alonso and Palacín, 2010; Palacín and Alonso, 2008). In spring males gather at traditional lek sites where they display to attract females for mating. Females nest at variable distances from the lek where they mated, and take over all brood-rearing duties. The chicks hatch by early June and follow their mothers during their first 6–18 months of life. During their first summer young birds are vulnerable to predators, and thus families show an elusive behaviour and tend to remain isolated from flocks of non-breeders. In the study area the species behaves as partial and differential migrants between breeding and post-breeding areas (Palacín et al., 2009). Great bustards are relatively long-lived (unpublished data), and show a poor capability to colonize new areas due to their marked philopatry, lek- and nest-site fidelity, and conspecific attraction (Alonso et al., 2004).

2.2. Study area and design

The study was carried out in central Spain, at two connected Special Protection Areas for birds (SPA; European Natura 2000 Network; European Commission, 2000) "Estepas cerealistas de los ríos Jarama y Henares" and "Estepas cerealistas de la Campiña", contained in the Important Bird Area (IBA) "Talamanca-Camarma" (40°N 3°W, 520 km^2, 792 a.s.l.; Fig. 1). This region is mainly agro-steppe landscape with a Mediterranean semiarid climate, dominated by extensive cereal (wheat and barley) cultures, and smaller patches of olive groves and legumes. It includes 16 villages and several small developments, with a relatively homogeneous size (mostly 50–250 pop/km^2). Due to its bird richness this area has been classified as a steppe bird "hotspot" in the Iberian Peninsula (Traba et al., 2007).

In October 2001 the construction of the Radial 2 (R2) four-lane highway began in the study area, to join the capital city of Madrid with Guadalajara. For this study we selected the 34 km highway sector that crosses both SPAs. The total amount of earth moved during this period was around 9,720,000 m^3. Inaugurated in October 2003, the traffic-volume is currently ca. 9500 vehicles/day with a traffic speed limit of 120 km/h (75 mph). Highway is not associated with any major natural barrier (e.g., mountain or river), is mostly hidden (through noise barriers or embankments) and fenced externally throughout its length.

To explore the changes in the distribution pattern of flocks-to-highway distances we applied a BDA design. We restricted the impact assessment to a 2 km buffer zone from the road, which falls within the reported road-effect distances for most published bird datasets (0–2580 m, Benítez-López et al., 2010; see Pruett et al., 2009 for other lekking birds). Road effect distances were analyzed using two approaches: as a continuous variable within the 2 km buffer, and dividing the buffer zone into four 500 m-wide bands (Fig. 1). For other analyses focused on population trends we applied a BDACI design, keeping the 2 km buffer as the impact zone (IZ).

Regarding the control zones, it is recommended that an intermediate zone be left between control and impact zones (e.g., Bro et al., 2004; Reijnen and Foppen, 1994), just as the monitoring of multiple control, ideally both near and far from the location of the intervention (Conquest, 2000). Thus, we chose a control zone (CZ1) whose edge is 2 km from the IZ and whose centroid is 7 km from the highway (Euclidean distance). We chose a second control zone (CZ2), separated from CZ1, whose centroid is 20 km from the highway and whose edge is at a minimum distance of 10 km from IZ. The habitat in both CZs was similar to that in the IZ, and the birds of all three zones belong to the same population, as concluded from radio-tracking and genetic studies (Alonso et al., 2004; Martín et al., 2002; Martín, 2008). The average bird abundances

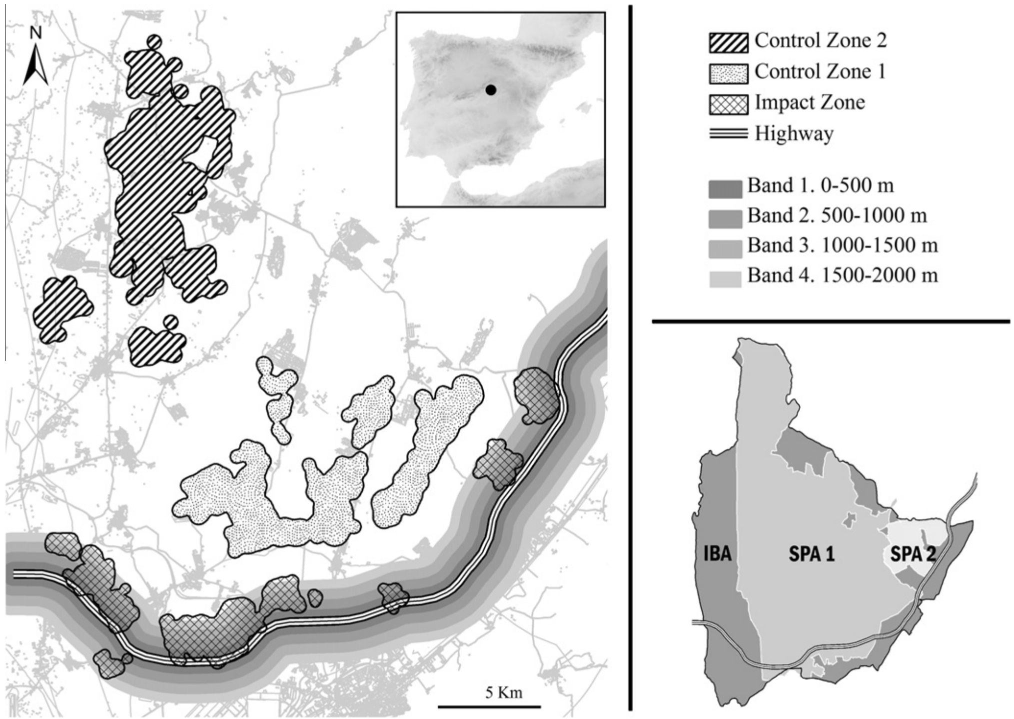

Fig. 1. Location of the study area in the Iberian Peninsula showing the impact and control zones of the effects of the highway construction, calculated through a 99% Kernel of all great bustard flocks observed during 1997–2009. The bands around the highway used to analyze the distance effect (see text) are also shown. The figure at the bottom right shows the main protected zones in the study area: "Estepas cerealistas de los ríos Jarama y Henares" (Special Protection Area for birds; SPA 1), "Estepas cerealistas de la Campiña" (SPA 2) and "Talamanca-Camarma" (Important Bird Area; IBA).

before highway construction were 251.5 (SD = 68.8) in the IZ, 195.5 (SD = 28.7) in CZ1, and 346.7 (SD = 50.3) in CZ2.

Landscape was relatively stable during the study period, except for the construction of the Radial 2 highway. We measured land-use change from 2000 to 2006 using CORINE Land Cover Changes 2000–2006 map (EEA, 2010), to confirm the low level of land use changes in the zones (2.6% in the impact zone, and 0% and 0.5% in the two control zones). Moreover, the length of roads other than R2 did not increase in any zone during the study period.

2.3. Bird surveys

Data were obtained from 49 censuses carried out by the same observers and using the same methodology, in 1997–2009. Each census was conducted by two or three teams of two people each, following pre-established itineraries with four-wheel drive vehicles and stopping frequently to scan for birds with binoculars and telescopes 20–60×. All great bustard flocks were mapped on 1:25,000 topographical maps. The censuses were done almost simultaneously within a year, thus minimizing the risk of double-counting individuals. Also, some birds were previously marked and we could identify the specific groups they belonged to. The total sample recorded was 1517 flocks (15,689 individuals). The first year was omitted in the analyses of demographic processes because the survey was incomplete in the control zones. We defined four seasons: winter (December to January), to provide the amount and distribution of wintering birds; spring (March, when the largest aggregations of individuals at lek sites, i.e., areas for male exhibition and mating, occur), to estimate the number of breeding individuals; early summer (July, when chicks are younger than 2 months and still following the females), to provide the amount and distribution of birds in summer; late summer (September, when the chicks have overcome the period of highest mortality), to give a second and more reliable estimate of the number of family groups, which by then are more visible.

2.4. Distances to highway analyses

We used the Euclidean distance to measure the distance to the highway from the locations of flocks, rather than those of individuals, because in gregarious species the behaviour of each individual in a flock is not independent from that of flock mates. Before carrying out the analyses we tested that there were no significant differences in mean number of bustards per flock among bands or construction phases (respectively, $H = 3.642$, $P = 0.162$, and $H = 5.046$, $P = 0.168$; Kruskal–Wallis test).

We explored distance effects considering three time scales: (1) whole year, based on all census observations, (2) seasonal, selecting the observations for each season, and (3) family groups in late summer. In the latter, we decided to use only family group observations to check whether their response was different, as a consequence of their particular ecological needs. We first aggregated the observations by bands to determine the spatial distribution along the highway, and to assess the possible changes between the three study phases: before, during and after construction of the highway (respectively, 1997–2001, 2001–2003, and 2003–2009). We constructed histograms for every phase with the relative frequency of observations aggregated by bands, and we evaluated the differences with χ^2 tests (*Rcmdr* package). All statistical analyses were done in R 2.10.1 statistical software (R Development Core Team, 2009).

In addition, we considered distance as a continuous variable and built Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990) with flock presence/pseudo-absence as the response variable and distance to highway as a predictor variable using binomial error structure and logit link. These models served to predict the species probability of presence according to the distance to the highway. The pseudo-absences were obtained from a map of potential habitat for the species, based on all census and sampling observations (Wisz and Guisan, 2009). First, we estimated the home range of great bustards following the cross-validated fixed kernel method (Seaman and Powell, 1997), using Hawth's Tools extension (Beyer, 2004) in ArcGIS 9.2 (ESRI). We defined the home range as the smallest area containing 99% of the observations. Next, in that area we subtracted the surfaces of buildings prior to highway construction. Then, we obtained the same number of random pseudo-absence points as presences (keeping equal weights on the presence and pseudo-absence data sets), applying a 100 m exclusion buffer (see Morales et al., 2008 for little bustard *Tetrax tetrax*) around each observation in order to minimize the probability that great bustards were using those parts of the territory. We created three univariate models, one for each phase, with smoothing splines of distance as the single nonparametric predictor (*mgcv* package; Wood, 2008).

Classification trees were built for presence/pseudo-absence of flocks with distance to road as a predictor variable (*Rpart* package), to determine the existence of threshold distances to highway (e.g., Palomino and Carrascal, 2007; Seoane et al., 2009), i.e., distances from the highway at which the probability of species presence increases substantially. These trees are nonparametric, hierarchical classifiers that predict class membership by recursively partitioning a data set into more homogeneous subsets (Breiman et al., 1984). In order to avoid excessively complex models and overfitting, different pruning procedures were performed to better generalize the predictive ability of the tree. Pruning was achieved (1) by eliminating nodes that increase errors in prediction within the pruning data set, (2) by statistically significant reductions of the group heterogeneity after each subdivision, and (3) by limiting the size of the tree to a maximum of six leaves (terminal tips). To evaluate the predictive ability we used the Correct Classification Rate (CCR; Fielding and Bell, 1997) to the whole tree, and the Negative Predictive Power (NPP; Fielding and Bell, 1997) to the first splitting criteria, which identifies the threshold distance.

2.5. BDACI analysis of population trends

To detect potential changes in population trends in the study area as a result of the highway construction, we analyzed the annual censuses of the bustard breeding population (March) during 1998–2009 with TRIM software (Pannekoek and Van Strien, 2005). TRIM computes population indexes that represent between-year changes, using 1998 as the base year. TRIM analyzes time series of counts using Poisson regression and accounts for overdispersion and temporal autocorrelation of data by estimating log-linear models with generalized estimating equations (e.g., Seoane and Carrascal, 2008; Wretenberg et al., 2007). TRIM models can take into account "change points", i.e., years when the overall trend of a series changes, and allow testing trends before and after particular change points. TRIM can also consider 'categorical covariates', i.e., factors that group individual sites on the basis of a feature hypothesized to affect population trends. To test whether population trends differed among phases we divided the data into the same three phases (i.e., 1998–2001, 'before'; 2002–2003, 'during'; and 2004–2009 'after'). Thus, years 1998, 2001 and 2003 were used as change points in linear (switching) trend models. We also considered 'zone' covariates as a factor with three levels to test whether population trends differed between impact (IZ) and control zones (CZ1 and CZ2). The Wald statistic (Harrell, 2001) was used to test the change points and covariate significance.

This resulted in twelve bustard population trends (i.e., three population trends for each zone and other three for the whole population). In addition, to test whether the population trends of each zone in the after construction phase ($n = 6$ years) differed from random population trends we tested the significance of the slope by resampling the regression of log-abundances on year. The slopes of the regressions with the original data were compared to a resampling distribution of slopes (resampling log-abundances 999 times within the zone). We did not use this method further in the other phases because of low sample size ('before': $n = 4$ years; 'during': $n = 2$ years).

2.6. BDACI analysis of family groups

Annual productivity values are highly variable in this species (Palacín, 2007), so we preferred to work with density of family groups, i.e., number of family groups (mother and 1–3 chicks) present in late summer divided by the surface of each zone as a surrogate variable, and test the differences in density of family groups between phases and zones.

3. Results

3.1. Distance effect of the highway

The distribution of great bustard flocks among the four 500 m bands considered changed significantly during the three phases: before, during and after the highway construction ($\chi^2 = 21.17$, d.f. = 6, $P = 0.002$). The main effect observed was a marked decrease in the use of the band nearest to the road (0–500 m) (53.4% during the construction phase and 56.9% after construction, with respect to the use before construction). Simultaneously, the number of flocks increased in the second band (500–1000 m) (respectively by 34.3% during and 54.6% after the construction). The changes in use of the third and fourth bands (1000–1500 m and 1500–2000 m) were less important, and combining both, the relative occupancy by flocks remained quite stable through the three construction phases (50–60%; see Appendix, Fig. A). We also found seasonal variability in the spatial distribution of flocks, although their distribution among bands did not statistically differ between the three phases in winter ($\chi^2 = 11.34$, d.f. = 6, $P = 0.078$) and late

Table 1
Deviance table of GAMs (binomial error structure) for road distance from whole year, seasonal and family group data. The models related the presence/pseudo-absence of great bustard locations with distance to the highway.

Models	Phase	Deviance explained (%)	N	χ^2	P
Whole year					
	Before	0.8	661	4.9	0.154
	During	9.6	288	27.1	0.000**
	After	7.7	805	57.0	0.000**
Seasonal					
Winter	Before	2.8	83	2.2	0.392
	During	22.5	40	8.2	0.043*
	After	12.7	130	13.8	0.016*
Spring	Before	1.3	217	2.7	0.329
	During	5.6	76	4.4	0.116
	After	4.7	207	10.3	0.024*
July	Before	5.5	128	7.0	0.080
	During	15.0	61	7.8	0.051
	After	7.3	189	14.8	0.003**
September	Before	0.5	233	0.8	0.637
	During	13.0	111	11.7	0.061
	After	8.3	279	22.0	0.002**
Family groups					
	Before	1.7	101	2.3	0.236
	During	24.0	44	9.3	0.030*
	After	9.2	111	9.4	0.074

Significance codes: $P > 0.5$; $^{*}P < 0.05$; $^{**}P < 0.01$.

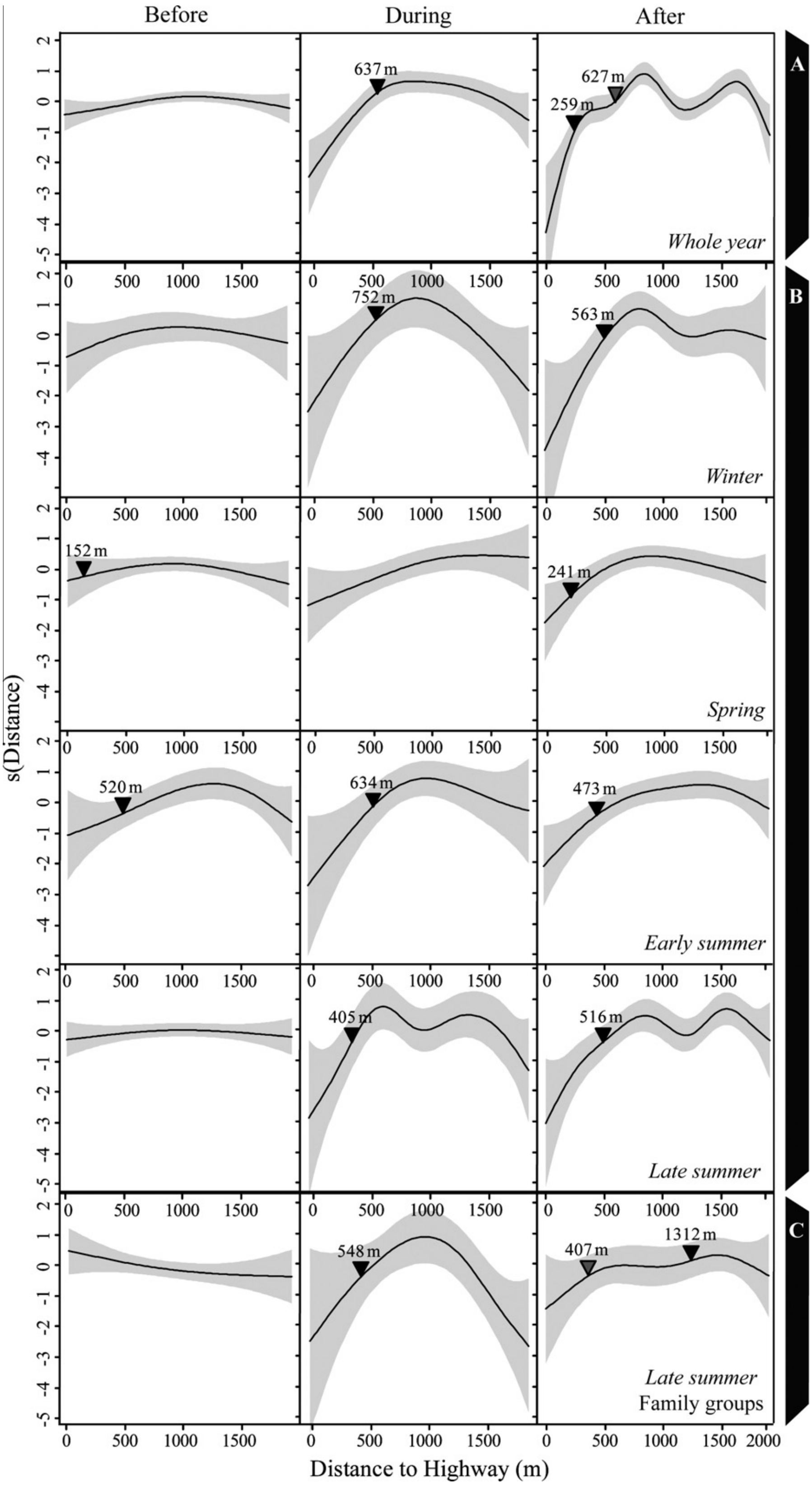

Fig. 2. Estimate response curves from predictive models and 95% confidence intervals of distance to highway (shading) on probability of presence, for the three periods considered: before, during and after the highway construction. The effects are in logit scale and standardized to mean equal to zero. The triangles mark the threshold distances selected by classification trees (main splittings = black triangles, secondary splittings = grey triangles). "A" row shows the models for whole year data, "B" for seasonal data and "C" for family groups.

summer (χ^2 = 12.36, d.f. = 6, P = 0.054), when the occupancy declined in the first band (respectively, 69.17% and 59.3%), neither in spring (χ^2 = 4.29, d.f. = 6, P = 0.637) and early summer (χ^2 = 5.89, d.f. = 6, P = 0.436), when the occupancy of band nearest to road was quite similar (respectively, from 15.18% to 11.32% and from 10.6% to 9.71%). Regarding family groups, differences among bands were significant (χ^2 = 24.31, d.f. = 6, P < 0.001), with very marked decreases in the use of the band closest to the highway during (73.1%) and after the road construction (68.4%; see Appendix, Fig. A).

In agreement with band use analyses, most GAM models relating flock presence/pseudo-absence to distance to the highway for the phases during and after construction were significant or marginally significant (Table 1). In contrast, no model for the before construction phase was significant, and the distance to the highway explained only 0.5–5.5% of the deviance (Table 1). The shapes of the values fitted from the models show that the spatial distribution changed markedly in all cases once the construction of the highway started (Fig. 2), with the exception of spring, when changes during and after construction were less pronounced. In general, the probability of presence was lower near the highway and increased progressively until reaching a certain threshold distance.

The classification trees allowed us to quantify the response threshold distances. We constructed 18 trees, of which 13 were significant and indicated the existence of threshold distances to highway (there were no significant threshold distances before the construction, except in spring and early summer). The trees that represented a year-long period identified a threshold distance of 637 m (TCC = 70%, NPP = 74%) during the construction, and two threshold distances of 259 m (TCC = 65%, NPP = 94%) and 627 m (NPP = 56%) respectively, after construction (see Appendix, Fig. B1).

GAM and tree models showed differences among seasons (Fig. 2). In winter, threshold distances were at 752 m (during phase: TCC = 73%, NPP = 64%) and at 563 m (after phase: TCC = 68%, NPP = 80%), and the GAM models for these two phases accounted for 22.5% and 12.7%, respectively, of the original deviance (Table 1). Early and late summer tree models were quite similar, showing threshold distances at 634 m (TCC = 75%, NPP = 82%) and 405 m (TCC = 64%, NPP = 88%) during construction, and 473 m (TCC = 64%, NPP = 78%) and 516 m (TCC = 60%, NPP = 75%) after construction, with a somewhat smaller percent of deviance explained (Table 1). Spring models were the least explanatory ones, with threshold distances around 200 m both before (TCC = 59%, NPP = 62%) and after construction (TCC = 58%, NPP = 100%). Finally, the tree models built with family groups showed the greatest differences between construction and operation phases. During the construction the GAM model accounted for 24% of the original deviance, with a threshold distance of 548 m (TCC = 63%, NPP = 75%; see Appendices, Fig. B2). However, after construction the main threshold distance reached 1312 m (TCC = 71%, NPP = 61%), with a secondary threshold at 407 m (NPP = 82%).

3.2. BDACI analysis of population dynamics

The TRIM model indicated that a significant slope change in population size occurred in 2003 (Wald test = 11.42, d.f. = 3, P = 0.009), i.e., when the construction phase finished. Change points in 1998 and 2001 were not significant (respectively, Wald test = 2.09, d.f. = 3, P = 0.553, and Wald test = 6.93, d.f. = 3, P = 0.074). Indeed, the population indices calculated by TRIM showed that population trends before and during construction were quite similar among the three zones (Table 2 and Fig. 3). During construction bird numbers increased significantly in all zones, i.e., the whole population was growing. In contrast, once the highway was built populations trends differed significantly among zones (Wald test = 33.88, d.f. = 3, P < 0.001): great bustards declined significantly in the IZ (from 363 to 211 individuals; Fig. 3), remained stable in CZ1 (mean [SD] = 220 [34] individuals), and increased significantly in CZ2 (from 411 to 567 individuals). Consequently, the overall population trend for the last phase was not significant but relatively stable with a slight trend to decrease (from 971 to 924 individuals; mean [SD] = 956 [49] individuals). In the impact zone the regression between log-abundance and year during the 'after' phase was significant (estimated by resampling) and showed a decreasing trend (Table 2). Year 2008 is an outlier (Bonferroni-adjusted t-test: P = 0.023), and year 2009 could be regarded as an influential point (Cook's Distance = 0.98, almost reaching 1, which is the common threshold at which to consider a point as influential in regression, Fox, 2008). However, the slope remains negative and significant even when removing either of the years (without 2008: slope = −0.07, d.f. = 3, P = 0.001, R^2 = 97.8%; without 2009: slope = −0.11, d.f. = 3, P = 0.022, R^2 = 86.5%). By contrast, the slope of year for the 'after' phase in CZ2 was significant and positive (estimated by resampling), and the slope in CZ1 was not significant. Year 2009 was also an outlier (Bonferroni-adjusted

Table 2
Annual population changes (in percentage) of great bustard in three zones (and the whole population) and three phases of highway construction, estimated by TRIM models of population trends and by resampling the regression of log-abundances on year. The last analysis was not applied for other phases because of low sample size ('before': n = 4 years; 'during': n = 2 years).

	TRIM results			Resampling results		
	% Annual population change	95% IC		% Annual population change	P	R^2
Before (1998–2001)						
IZ[a]	−2.67	−8.81	3.47	–	–	–
CZ1[b]	−6.86	−15.9	2.18	–	–	–
CZ2[c]	−8.99*	−17.07	−0.91	–	–	–
Whole	−3.61	−8.8	6.77	–	–	–
During (2002–2003)						
IZ	17.6*	8.73	26.47	–	–	–
CZ1	16.99*	5.65	28.33	–	–	–
CZ2	10.67*	1.33	20.01	–	–	–
Whole	15.32*	7.46	23.18	–	–	–
After (2004–2009)						
IZ	−8.54*	−10.93	−6.15	−9.18	0.008**	0.73
CZ1	−4.01	−8.04	0.01	−1.79	0.150	0.14
CZ2	11.54*	7.79	15.29	6.41	0.017	0.68
Whole	−0.01	−2.95	1.57	−3.45	0.298	0.04

Significance codes: P > 0.5; *P < 0.05; **P < 0.01.
[a] IZ, impact zone.
[b] CZ1, control zone 1.
[c] CZ2, control zone 2.

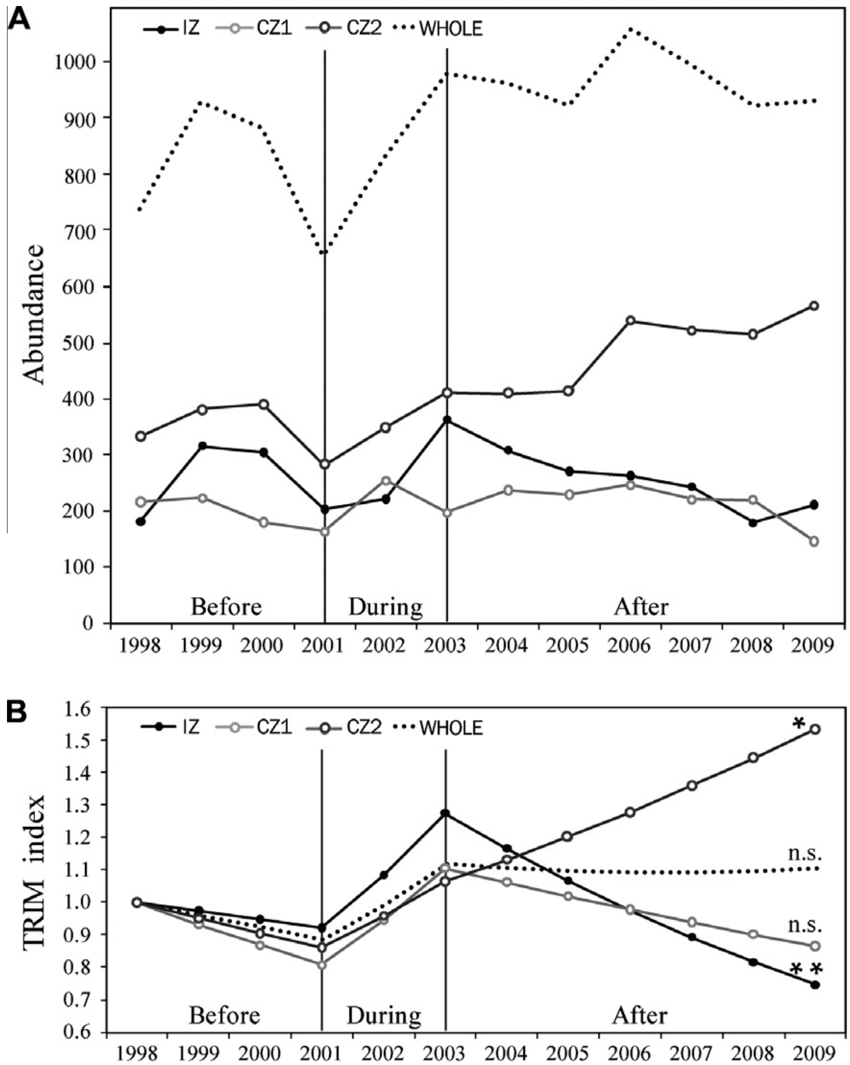

Fig. 3. (A) Temporal variation of the great bustard abundance. (B) TRIM model-predicted population indexes (the "1" in the *y*-axis stands for the initial population sizes at the three zones) for each zone (IZ = impact zone, CZ1 = control zone 1, CZ2 = control zone 2; WHOLE = Whole Population). Vertical bars denote the three phases: 'before' (1998–2001), 'during' (2002–2003) and 'after' (2004–2009) construction of the road. The significance of the slope of each zone in the 'after' phase is shown by resampling the regression of log-abundances on year: Significance codes: n.s. ($P > 0.5$); *($P < 0.05$); **($P < 0.01$).

t-test: $P = 0.052$) for CZ1 and was a highly influential point (Cook's Distance = 2.04). Hence, we decided to remove this observation because it had a high weight in the slope of the population trend (with 2009: slope = −0.08, d.f. = 4, $P = 0.09$, $R^2 = 43.5\%$; without 2009: slope = −0.02, d.f. = 3, $P = 0.288$, $R^2 = 14.2\%$). In brief, the trend for the whole great bustard population during 'after' phase was not significant (slope = −3.45, d.f. = 16, $P = 0.298$, $R^2 = 3.9\%$).

Concerning productivity, the density of family groups varied widely during the study period (IZ, CZ1 and CZ2 had mean densities of, respectively, 0.31 [SD 0.17], 0.51 [SD 0.18] and 0.65 [SD 0.30]), although the density recorded in the IZ was smaller than in both control zones. However, the trends were similar among zones, with years of marked growth and years of steep falls. The density did not differ significantly among construction phases (ANOVA, $F = 0.02$, $P = 0.982$) and changes were concomitant among zones (the phase-zone interaction was not significant either $F = 0.48$, $P = 0.752$).

4. Discussion

Our study exemplifies the conflict between conservation goals and the growth of road networks. The results showed that great bustard use of areas near a highway decreased during and after road construction, implying a significant loss of habitat for this species. Demonstrating road effects on wildlife has been challenging, due to methodological limitations or study design flaws (Balkenhol and Waits, 2009; Benítez-López et al., 2010). BACI designs are strongly recommended as the most powerful tools to avoid most of these flaws and to clearly identify the effects of human infrastructures (Roedenbeck et al., 2007; Stewart-Oaten and Bence, 2001). To our knowledge, this is one of the first studies using BDA and BDACI designs to determine the effects of the construction of a highway on an animal population. All studies about road effects, including those using BACI, are biased to some extent, because the impact zone is nonreplicable (Stewart-Oaten and Bence, 2001; Underwood, 1992), and roads are not randomly distributed across the landscape because their location is planned according to topographic and others suitability criteria (Stewart-Oaten and Bence, 2001). This means that it will be difficult to extrapolate conclusions from non-randomly selected sites. In spite of this difficulty, the BACI approach is still recommended when a time series including data before the intervention is available for both the impact zone and control zones (Roedenbeck et al., 2007; Stewart-Oaten and Bence, 2001). Some authors have suggested caution when interpreting results, particularly when few species change their behaviour or the responses detected are not strong, because in such cases it would be difficult to discard the effects of alternative potential causal factors (Schroeter et al., 1993). In our study, however, we could clearly identify and measure the avoidance behaviour of great bustards, and detect a marked change in the species' population trend in the impact zone.

4.1. Distance effect from highway and seasonal patterns of threshold distances

The combination of GAM and tree models has proven to be a useful framework for obtaining a realistic representation of the species' response to the road construction. This approach could likely be applied to all linear infrastructures with others species. Furthermore, as opposed to analysis by bands, this procedure avoids the problems derived from a subjective delimitation of bands. Although explained deviance may seem low, the models are univariate. Also, values adjusted by the model suggest that distance to road has a considerable effect up to a certain distance, while farther away from the road other variables have an effect on the presence/absence of flocks. In other words, distance is an important explanatory variable for a limited sector of the 2 km band, which reduces the total variance explained. Indeed, the predictive capacity of threshold distances obtained from classification trees was much higher (NPP averaged roughly 80%). Overall, the threshold distances in the models averaged *ca.* 630 m from the highway, with a minimum occupancy within 259 m. The greatest changes in the spatial distribution happened within the 1000 m band nearest to the road, with a possible local movement from the 0–500 m to the 500–1000 m band.

Several studies have shown that animals respond in different ways to different types of human activities, depending on certain characteristics like speed, noise, or the potential danger these activities imply (Riddington et al., 1996; Sastre et al., 2009). In our case, the distance effect became apparent during the construction, and later also during the operation phase, which suggests that both building activities and car traffic caused avoidance behaviour in the great bustard.

The response of great bustards was not the same in all phases of their annual cycle. Threshold distances were highest during winter, whereas GAM and tree models obtained in spring were not sufficiently explanatory to suggest a considerable effect during this season. These results agree with a previous habitat selection study showing that winter locations are less fixed than lek sites in this species, and located at greater distances from the nearest roads (Palacín, 2007). A plausible explanation is that in spring, the distribution of great bustards is strongly conditioned by the need to aggregate at traditional lek sites (Alonso et al., 2000). Strong site fidelity has also been reported for most lekking species (Höglund and Alatalo, 1995). Great bustards showed a clearly avoidance behaviour in summer as well. Particularly family groups were less tolerant, as shown by their higher distance effect as compared to flocks, with a low occupancy up to 1300 m. Mothers probably prioritized minimizing risks for their offspring, and thus selected territories far from road disturbances.

Some studies with other species also reported that responses to road disturbances may change throughout the year. For example, seasonal patterns have been described for roadkills and related to seasonal changes in habitat preferences or dispersal movements (Grilo et al., 2009; Smith-Patten and Patten, 2008). Traffic-volume and noise have often been considered the most decisive factors causing changes in bird distribution patterns near roads (Forman et al., 2002; Reijnen and Foppen, 2006). Our study area was quite noisy long before the road construction began, due to the presence of a nearby airport, so the avoidance behaviour could be more related to the construction works and traffic volume. However, the absence of substantial seasonal fluctuations in traffic volume (mean [SD] = 7437 [3152] vehicles/day in winter, 9009 [3724] vehicles/day in spring, 10 116 [3218] vehicles/day in early summer and 9321 [3100] vehicles/day in late summer; data from the highway company HENARSA), suggests that the temporal pattern in bird distribution could depend on other behavioural features of the species.

4.2. Changes in population dynamics

The analyses of population trends and productivity combining TRIM and BDACI allowed us to ascertain any changes in population size, a crucial issue for conservationists (Gill et al., 2001; Sutherland, 1996). Population trends observed prior to and during road construction were rather similar in the impact zone and both control zones, and they also coincided with overall trends in a much wider region (Martín, 2008). In contrast, after the highway construction there was little agreement in the population trends between impact and control zones. During the construction the whole population was growing and suddenly in 2003 (when the highway was fully operative) the trends changed: the population gradually declined in the impact zone, while it remained stable in the closest control zone and increased in the farthest. This suggests that a new process would be affecting population dynamic. Neither a potential decrease in productivity in the impact zone, which was smaller than in both control zones through the whole study period, nor roadkills, which have never been reported in our study area, seemed to contribute to that population decline. A more plausible explanation, which is supported by the general stability of the whole great bustard population in our study area and in a wider region (Martín, 2008; unpublished data), is that a number of birds could have moved from the impact zone to the farthest control zone as a consequence of the road construction. Studies based on extensive radio-tracking of marked individuals (Alonso et al., 2004; Martín et al., 2008) have shown that the settlement of dispersers is highly determined by the presence of conspecifics (i.e., through conspecific attraction, see Danchin and Wagner, 1997), thus we suggest that the lower disturbance levels and the higher number of conspecifics in the farthest control zone were decisive in the population changes observed.

4.3. Methodological aspects

The methodological framework including a long-term series of surveys and BDA and BDACI designs has allowed us to detect and quantitatively assess the effects of the road construction with high inferential strength. In addition, the selection of two control zones at different distances from the highway was useful to identify and confirm some road effects and to understand the bird responses at the scale of the whole population. We strongly recommend using such a variable range of spatial scales in future impact studies.

BDACI design can be applied in Road Ecology to assess both road effects and effectiveness of mitigation measures. However, ecological impact assessments are usually conducted under time constraints that make the collection of previous data and application of BDACI design difficult. Unfortunately, feasibility of the studies declines with the inferential strength, because of the greater number of design requirements that must be fulfilled and the number of resources required to fulfill them (Roedenbeck et al., 2007). BDA design would appear to work well only for assessing population changes for temporally invariant taxa (i.e., those in steady-state equilibrium; Wiens and Parker, 1995), because the assessor would expect the population trends to be equal in the absence of highway, assuming that natural variation is similar between before, during and after sampling phases. Regarding CI design, the difference between impact and control zones is valid only if control and impact zones are identical in the absence of highway, an assumption that cannot be tested, because the before-after component is missing (Osenberg and Schmitt, 1996). If our study had started when the road was opened to traffic it would have detected a population decrease in the impact zone. However, it would not be clear whether such decrease was a consequence of previous population trends, which in such a study would be unknown. In the end, the research question addressed and the study species (temporal dynamic, recovering rates, spatial distribution, etc.) will determine the particular study design selected and the length of monitoring program (see a hierarchy of study designs in Roedenbeck et al., 2007).

4.4. Conclusions and management implications

The current and future trends of agro-steppe landscapes may be explained by three change vectors: urbanization, agricultural intensification and land abandonment (Santos and Suárez, 2005). Southern European countries still hold well-preserved agro-steppe areas, but the increasing construction of infrastructures (e.g., highways, railroads or power lines; e.g., Martínez-Abraín et al., 2009) and urban sprawl are one of the highest threats of habitat fragmentation, which may imply serious risks for endangered species living in these areas. Regarding protected areas, this study highlights the conflicts between conservation efforts and expansion of the infrastructures. Hence, there is an increased need for management proposals to enforce the policy concerning the Natura 2000 network. Member states of European Union have to take appropriate steps to avoid deterioration of habitat or any disturbances affecting birds (Directive 2009/147/EC), so they must pay more attention to new linear infrastructures.

In the present work, although the effects of the highway did not necessarily imply a decrease in the overall population size, they caused changes in the space use patterns of species, and ultimately contributed to a higher aggregation, which might in turn lead to a loss of genetic diversity, as well as a higher vulnerability due to demographic and environmental stochasticity (Epps et al., 2005). Our results contributed to increasing the knowledge about the functional responses of great bustards to roads, and to quantifying some of the negative effects of these infrastructures, thus they should be considered when planning and evaluating alternative road alignments.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.05.014.

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