Bird Conservation International (2011) 21:303–310. © BirdLife International, 2011
doi:10.1017/S0959270911000128

Estimating the impacts of power line collisions on Ludwig's Bustards *Neotis ludwigii*

ANDREW R. JENKINS, JESSICA M. SHAW, JON J. SMALLIE, BRADLEY GIBBONS, RONELLE VISAGIE and PETER G. RYAN

Summary

Ludwig's Bustard *Neotis ludwigii*, endemic to Africa's south-west arid zone, is susceptible to collisions with overhead power lines. Limited data from the south-eastern part of its range suggest that this factor may threaten its survival. We estimated transmission line collision rates for Ludwig's Bustard across its South African range to assess the effect of this mortality on the population. Conservatively, collision rates averaged at least 0.63 ± 0.12 fatal collisions per km of transmission line per year, with relatively little regional variation. Despite being less abundant, the larger males were more collision-prone than females, which might account for the female-biased population. Extrapolating collision rates across the range of the species suggests that 4,000–11,900 birds are killed annually on high-voltage transmission lines. Actual mortality on overhead lines is probably much greater, given biases in carcass detection (crippling, scavenging and habitat biases), as well as the fact that our estimate excludes mortality on lower voltage distribution lines and telephone wires. Given an estimated global population of 56,000–81,000 birds in the late 1980s, the demographic invariant method suggests that such mortality is unsustainable. This result supports the recent upgrading of the conservation status of Ludwig's Bustard from 'Least Concern' to 'Endangered', and highlights the need for further research on this problem.

Introduction

Ludwig's Bustard *Neotis ludwigii* is endemic to the arid zone of south-west Africa, ranging from extreme south-west Angola through Namibia to the Karoo scrublands of western South Africa, occasionally reaching south-west Botswana and Lesotho (Allan 1997, Fig. 1). Its total range is roughly 380,000 km^2 but it occurs patchily, moving in response to local rainfall patterns (Herholdt 1988, Allan 2005). Allan (1994) estimated the global population in the late 1980s to be 56,000–81,000 birds, with at least half of these occurring in South Africa. The species is listed 'Vulnerable' in South Africa due to the impacts of collisions with overhead wires and hunting (Barnes 2000).

As a large (up to 6 kg), open-country species that undertakes daily flights to and from roost sites as well as longer distance movements (Allan 2005), it is particularly susceptible to collision with overhead lines. Surveys in the eastern Karoo in the late 1990s found that Ludwig's Bustards comprised almost half of all birds killed by colliding with power lines (Anderson 2001), with bustard collision rates of 0.5–2 birds km^{-1} year^{-1} (M. D. Anderson unpubl. data). They also are killed by colliding with other overhead wires (Herholdt 1988), with telephone lines accounting for 23% of collision mortalities in one study (Allan 2005). Given that 17,000 km of high voltage transmission lines (≥ 132 kV) cross the species' range (see methods for details), as well as thousands more kilometres of low-voltage distribution lines and telephone lines, there is an urgent need to assess whether the collision rates reported for the eastern Karoo occur throughout the range. In this paper we estimate collision rates for six sections of transmission lines in the

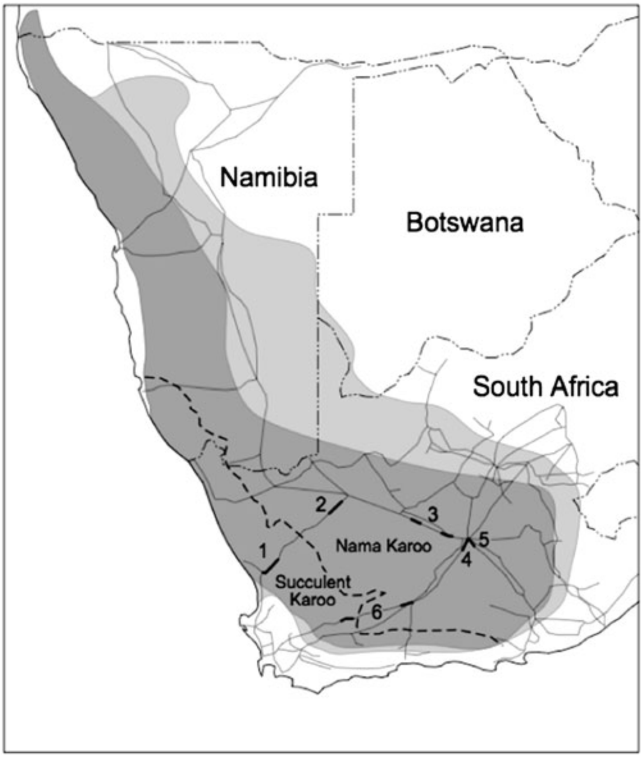

Figure 1. The distribution and relative abundance of Ludwig's Bustard (two tone shading based on atlas reporting data, Allan 1997) and high voltage transmission lines (≥ 132 kW) in its range. Bold segments show lines surveyed for bustard collision remains in the Knersvlakte (1, Helios-Juno), Bushmanland (2, Aries-Helios), eastern Nama Karoo (3, two sections of the Hydra-Kronos line, 4, Droërivier-Hydra and 5, Hydra-Poseidon), and two sections of the Droërivier-Muldersvlei line in southern Karoo (6).

Succulent and Nama Karoo of South Africa. We use the demographic invariant method (Niel and Lebreton 2005) to assess whether the extrapolated mortality is sustainable.

Methods

Bustard collision rates were estimated at six sites across Ludwig's Bustard range in South Africa (Fig. 1). All surveys were conducted along 400 kV transmission lines because they have four-wheel-drive tracks running beneath the lines, facilitating access. After initial clearing of carcasses, repeat surveys were made to assess the mortality rate of bustards. At two sites near De Aar in the eastern Nama Karoo, three repeat surveys were made at 2–6 month intervals from May 2008 (49 km of the Hydra-Poseidon line) and August 2008 (63 km of the Droërivier-Hydra line; Table 1). At the other four sites, initial clearing took place in early May 2009, with repeat sampling three months later in early August 2009 (Table 1). These sites were located in the Knersvlakte bioregion of the Succulent Karoo, between the Helios and Juno substations (53 km), in the Bushmanland bioregion of the western Nama Karoo (Aries-Helios, 54 km), in the eastern Nama Karoo (Hydra-Kronos, 49 km) and along two sections of the Droërivier-Muldersvlei/ Bachus line (70 km) in the southern Nama and Succulent Karoo (Table 1).

Table 1. Crude collision rates (birds $km^{-1}.year^{-1}$) for Ludwig's Bustards at six sites along 400 kV transmission lines in the Karoo, South Africa (listed in order numbered on Fig. 1).

Site (length of line)	Sampling interval	Bustards killed	Rate (birds $km^{-1}.yr^{-1}$)
1. Helios-Juno (53 km)	May–Aug 2009 (3.0 months)	9	0.68
2. Aries-Helios (54 km)	May–Aug 2009 (3.0 months)	6	0.44
3. Hydra-Kronos (49 km)	May–Aug 2009 (3.0 months)	13	1.06
4. Droërivier-Hydra (63 km)	Aug–Oct 2008 (2.5 months)	10	0.76
	Nov 2008–Mar 2009 (4.8 months)	5	0.20
	Apr–July 2009 (4.0 months)	38	1.81
	Total (11.3 months)	53	0.89
5. Hydra-Poseidon (49 km)	May–Sept 2008 (4.5 months)	7	0.38
	Oct 2008–Mar 2009 (6.0 months)	6	0.24
	Apr–July 2009 (4.0 months)	9	0.55
	Total (14.5 months)	22	0.37
6. Droërivier-Muldersvlei (70 km)	May–Aug 2009 (3.0 months)	6	0.34
All lines (338 km)		109	0.63

Surveys were conducted from a vehicle with a driver and at least one observer scanning the area ahead and 5–15 m to the side of the vehicle for collision remains. We opted to drive rather than walk the surveyed lines to cover as much line as possible. The vehicle was driven slowly (about 10 km h^{-1}), taking 1–2 days to cover each section. Fresh remains usually were accompanied by large numbers of feathers, making them fairly conspicuous. All carcasses were photographed *in situ* and their positions recorded by GPS. Samples were collected to sex carcasses on most surveys; Ludwig's Bustard males average 20% larger (mean wing chord: females 465 mm, males 551 mm; mean tarsus length: females 120 mm, males 139 mm; Allan 2005) and 80% heavier than females (females 2.2–3.0 kg, males 3.1–6.0 kg; Allan 2005), so their sex can be inferred from the size of major bones and flight feathers. Identification and sexing was verified using the comparative collections from the Iziko Museum, Cape Town.

Minimum collision rates (bustards killed per km of transmission line per year) were estimated based on numbers of fresh carcasses encountered, expressed in terms of the distance of line surveyed and the time between surveys (collision rate = number of dead bustards/line length sampled in km/sample interval in years). These are minimum values because they ignore biases in carcass detection (Bevanger 1998, Janss 2000, Janss and Ferrer 2000): the proportion of birds crippled in collisions which moved off the survey strip before dying and hence remained undetected (crippling bias) and the proportion of collision victims that died within the survey strip that were removed from the survey strip by scavengers (scavenging bias) or were obscured by vegetation and not detected (habitat bias).

Demographic impacts

To model the demographic impact of power line mortality on the population of Ludwig's Bustard, we needed to determine the length of power lines within its range, the number of bustards and key life history parameters. ArcView 3.2 (ESRI 1999) was used to estimate the length of all high-voltage transmission lines (≥ 132 kV) crossing the species's range in South Africa and Namibia (Allan 1997, Fig. 1). Data for transmission lines were supplied by national electricity supply companies (Eskom and NamPower). We estimated minimum bustard mortality on transmission lines each year by extrapolating the observed collision rate recorded in our study across its range. Our surveys were confined to the core range of the species (Fig. 1), so we arbitrarily assumed collision mortality rates were 50% lower in the periphery of its range, to account for predicted lower densities of bustards. Varying this assumption had little impact on the final conclusions. The sustainability of this mortality was assessed given a global population of Ludwig's Bustard of 56,000–81,000 individuals in the late 1980s (Allan 1994).

Few demographic data are available for Ludwig's Bustard (Allan 2005) so we used the demographic invariant method (DIM) (Wade 1998, Niel and Lebreton 2005). In the absence of accurate demographic information, the DIM estimates whether anthropogenic mortality is sustainable by comparing the potential excess growth of a population increasing at its maximum rate with the number of individuals lost to unnatural mortality (Niel and Lebreton 2005, Dillingham and Fletcher 2008). It uses adult survival (s) and age of first reproduction (α) to predict maximum annual growth rate (λ_{max})

$$\lambda_{\max} \approx \frac{(s\alpha - s + \alpha + 1) + \sqrt{(s - s\alpha - \alpha - 1)^2 - 4s\alpha^2}}{2\alpha}$$

which is then used to infer the potential excess growth as $N\beta(\lambda_{max}\text{-}1)$, where N is the population size and β accounts for the effect of density on demographic performance and protects against biases in parameter estimation (Niel and Lebreton 2005, Dillingham and Fletcher 2008). The maximum value of $\beta = 0.5$ (Niel and Lebreton 2005), but it has been suggested to use $\beta = 0.3$ for near threatened species and $\beta = 0.1$ for threatened species (Dillingham and Fletcher 2008).

Unfortunately, there are no estimates of adult survival or age of first reproduction for Ludwig's Bustards, so we were forced to select a range of plausible values. Adult survival and age of first reproduction are known for three Eurasian bustards: Great Bustard *Otis tarda* (females 3.5–4.5 kg, males 7–15 kg; Cramp 1980) has $s \approx 0.9$ and $\alpha = 3$ (Alonso *et al.* 2004), Houbara Bustard *Chlamydotis macqueenii* (females 1–2 kg, males 1.5–3 kg; Cramp 1980) has $s \approx 0.9$ and $\alpha = 1$ (Combreau *et al.* 2001), and Little Bustard *Tetrax tetrax* (both sexes 0.7–0.9 kg; Cramp 1980) has $s \approx 0.7$ and $\alpha = 1$ (Bretagnolle and Inchausti 2005, although survival estimates may include some human-induced mortality). Ludwig's Bustards (females 2–3 kg, males 3–6 kg; Allan 2005) are intermediate in size between Great and Houbara Bustards, so their adult survival is expected to be similar ($s \approx 0.9$), but it is unknown at what age females start to breed.

Results

Initial clearing of the 338 km of power lines located 181 Ludwig's Bustard carcasses (0.54 bustards km^{-1}). Repeat surveys found 109 bustards at an average rate of 0.63 ± 0.12 (SE) bustards km^{-1} power line yr^{-1} (Table 1). Treating repeat surveys of the two De Aar lines as independent samples had little effect on the average mortality rate (0.65 ± 0.15 bustards km^{-1} yr^{-1}). Mortality rates around De Aar peaked in autumn (April–July: average 1.18 bustards km^{-1} yr^{-1}) when some birds move west with winter rainfall in the Succulent Karoo (Allan 1997), but there was no evidence of an increase linked to birds returning east in early summer. Collision rates were lower in summer (Sept/Oct–March: 0.22 bustards km^{-1} yr^{-1}) than in winter (May–Sept/Oct: 0.57), but this may be biased in part by the longer sampling interval during summer, resulting in an increase in scavenge and habitat biases. Overall, 82% (n = 89) of bustards were sexed, of which

61% were males and only 39% females. This is significantly different from a 1:1 sex ratio ($\chi^2_1 = 4.07$, $P < 0.05$) and is much greater than the female-biased population reported by Allan (1994; $\chi^2_1 = 13.25$, $P < 0.001$).

Estimating the impact of collision mortality

Currently some 17,000 km of high-voltage transmission lines cross the range of Ludwig's Bustard, of which 60% are in the core of the species's range (Fig. 1). Most (71%) of the transmission lines are in South Africa. Simple extrapolation suggests that at least 6,500 (95% CI 4,000–9,000) bustards are killed annually by transmission lines in the core range of the species. If the rate of collision mortality in the periphery of its range is half that in the core area, minimum annual mortality increases to 8,600 (5,300–11,900) bustards per year. Assuming the population remains the same as it was in the late 1980s (56,000–81,000 birds; Allan 1994), at least 11–15% of the bustard population is killed by colliding with transmission lines each year. Given male biased mortality and a female biased population, at least 7–10% of female and 16–22% of male bustards are killed in collisions each year. If the population has decreased since the late 1980s, these proportions will be even greater. These estimates exclude sampling biases (crippling, scavenging and habitat biases) as well as birds dying on lower voltage distribution lines and telephone wires.

The proportion of additional mortality predicted to be sustainable by the demographic invariant method is most sensitive to the age of first reproduction. Assuming Ludwig's Bustards have adult survival of 0.9, for β=0.5 they can sustain at most 16% additional mortality if females start breeding after 1 year, 10% if they breed after 2 years, and 8% if they breed after three years, but this falls still further if a smaller value of β is used (Table 2). In the absence of even crude estimates of demographic parameters there is considerable uncertainty as to the levels of mortality that can be sustained, but the most plausible scenarios currently predict that the population should be decreasing, probably quite rapidly.

Discussion

Objects in the landscape, such as power lines and wind turbines, have the potential to significantly increase mortality rates in large-bodied species, particularly raptors and bustards (Tellería 2009, Jenkins *et al.* 2010, Rollan *et al.* 2010 or to impact on flight behaviour (Raab *et al.* 2011)). Allowing for temporal variation in collision frequency, which probably reflects the erratic nature of Karoo conditions and the nomadic nature of Ludwig's Bustards (Allan 2005), estimates of collision mortality were quite similar for all six areas sampled (Table 1; range 0.34–1.06 birds km^{-1} yr^{-1}).

Table 2. Sustainable additional mortality as a % of total population size estimated using the demographic invariant method, for β = 0.5, 0.3 and 0.1 (see methods for details).

Adult survival (*s*)	Female age of first reproduction (α)								
	B = 0.5			β = 0.3			β = 0.1		
	1	2	3	1	2	3	1	2	3
0.70	27	16	12	16	10	7	6	3	2
0.75	25	15	11	15	9	7	5	3	2
0.80	22	14	10	13	8	6	5	3	2
0.85	19	12	9	12	7	5	4	2	2
0.90	16	10	8	10	6	5	3	2	2
0.95	11	7	6	7	4	3	2	2	1

Recent observations in Namibia by the NamPower/Namibian Nature Foundation Strategic Partnership indicate that Ludwig's Bustards also are affected by power line collisions in that country. These results confirm that collisions are a serious cause of mortality throughout the bustard's range. Our data were collected over large areas of relatively homogeneous habitat, whereas most published studies in this field present collision rates for relatively short sections of line adjacent to localised patches of habitat or points of aggregation for collision-prone birds (Jenkins *et al.* 2010). Consequently we believe we are justified in extrapolating from our data across the species's range.

Our data are minimum estimates of actual mortality on transmission lines, given biases in line surveys (Bevanger 1998, Janss 2000, Janss and Ferrer 2000). Estimating these biases is time-consuming and complex, and was not feasible for our study. Other studies have simply used conservative values based on published estimates (e.g. Sundar and Choudhury 2005, Shaw *et al.* 2010). In the Karoo, scavenging bias is likely to be significant given the large populations of small and medium-sized mammalian predators. Habitat bias was increased by driving rather than walking under lines, reducing the detection rate for carcasses particularly in areas where rough terrain and dense vegetation hampered vehicle-bound observers. Taken together, it is likely that our surveys substantially underestimated actual kill rates (Bevanger 1995).

We only estimated collision rates on high voltage transmission lines, but bustards also are killed after colliding with other overhead wires. Opportunistic records of power line mortality recorded over the last 12 years in South Africa by the Eskom/Endangered Wildlife Trust Strategic Partnership include 228 Ludwig's Bustard collisions, of which almost half (46%) occurred on distribution lines (≤ 66 kV). Also, power lines are not the only source of collision mortality. For example, telephone wires were estimated to account for 23% of Ludwig's Bustard mortality in the late 1980s (Allan 2005). Given these additional sources of collision mortality and the likely survey biases which could not be estimated in our study, our estimate of transmission line mortality probably represents only 20% of the actual mortality on overhead wires.

Any assessment of the impact of collision mortality on the population of Ludwig's Bustard is hampered by the lack of demographic data for the species. Parameters from similar-sized bustards suggest that sustainable mortality cannot exceed 16%. However this may be optimistic, because a population viability analysis for the smaller Houbara Bustard estimated that human-induced mortality could not exceed 7.2% per year (Combreau *et al.* 2001). The crude estimate of transmission line mortality alone represents 11–15% of the estimated Ludwig's Bustard population in the late 1980s. If the population has decreased since then, the current mortality will be an even larger proportion of the total population. Unfortunately there are no count data to assess the current population of Ludwig's Bustards. However, collision rates on transmission lines near De Aar have fallen from 1.5 to 1.6 bustards km^{-1} yr^{-1} in 1998–2001 (M. D. Anderson unpubl. data) to 0.62 in 2008–2009 (this study), possibly at least in part as a result of a decrease in bustard numbers.

Given that our estimate of transmission line mortality represents perhaps only 20% of total collision mortality, it is likely that the species is under severe threat. One factor perhaps operating in its favour is that male Ludwig's Bustards apparently are more prone to power line collisions than females. This probably occurs because males are much larger, heavier and less able to avoid aerial obstacles (Janss 2000, Jenkins *et al.* 2010), and it may explain the female bias among Ludwig's Bustards (Allan 2005). Similar male-biased collision mortality has been suggested to exaggerate female-biased sex ratios among local populations of Great Bustards (Martín *et al.* 2007). Given the polygamous mating system (Allan 2005), loss of males will have less demographic impact than loss of females, provided the population remains reasonably large. However, scavenging bias may be greater for smaller female bustards, so we may have overestimated male bias.

Clearly, more data are needed to resolve the conservation status of Ludwig's Bustard. Priorities include a repeat survey of the population and estimating key demographic parameters such as the age of first reproduction and survival. However, these preliminary data support the recent up-listing of Ludwig's Bustard on the IUCN Red List (http://www.iucnredlist.org/apps/redlist/-search). Under criterion A4, the species qualifies as globally 'Endangered', based on an estimated decline of 50–79% over three generations. This measure should help to stimulate further research and conservation action to reduce power line collisions and thus improve the conservation status of the species.

Acknowledgements

Koos de Goede, Zelda Bate and Ruben Jenkins-Bate assisted ARJ in the field. Graham Avery of Iziko Museums, Cape Town, helped to identify collision remains. This work was funded by Eskom's Research & Development Division; we thank Michael D. Michael for his ongoing support as well as Eskom staff and the landowners of the Karoo for their cooperation.

References

Allan, D. G. (1994) The abundance and movements of Ludwig's Bustard *Neotis ludwigii*. *Ostrich* 65: 95–105.

Allan, D. G. (1997) Ludwig's Bustard. Pp. 350–353 in: J. A. Harrison, D. G. Allan, L. G. Underhill, M. Herremans, A. J. Tree, V. Parker, and C. J. Brown, eds. *The atlas of southern African birds. Vol. 1: Non-passerines*. Johannesburg: BirdLife South Africa.

Allan, D. G. (2005) Ludwig's Bustard. In: P. A. R. Hockey, W. R. J. Dean and P. G. Ryan, eds. *Roberts birds of southern Africa, VII*. Cape Town: John Voelcker Bird Book Fund.

Alonso, J. C., Martín, C. A., Alonso, J. A., Palacín, C., Magaña, M. and Lane, S. J. (2004) Distribution dynamics of a Great Bustard metapopulation throughout a decade: influence of conspecific attraction and recruitment. *Biodivers. Conserv.* 13: 1659–1674.

Anderson, M. D. (2001) The effectiveness of two different marking devices to reduce large terrestrial bird collisions with overhead electricity cables in the eastern Karoo, South Africa. Johannesburg: Draft report to Eskom Resources and Strategy Division.

Barnes, K. N. (2000) *The Eskom Red Data Book of birds of South Africa, Lesotho and Swaziland*. Johannesburg: BirdLife South Africa.

Bevanger, K. (1995) Estimates and population consequences of tetraonid mortality caused by collisions with high tension power lines in Norway. *J. Appl. Ecol.* 32: 745–753.

Bevanger, K. (1998) Biological and conservation aspects of bird mortality caused by electricity power lines: a review. *Biol. Conserv.* 86: 67–76.

Bretagnolle, V. and Inchausti, P. (2005) Modelling population reinforcement at a large spatial scale as a conservation strategy for the declining Little Bustard (*Tetrax tetrax*) in agricultural habitats. *Anim. Conserv.* 8: 59–68.

Combreau, O., Launay, F. and Lawrence, M. (2001) An assessment of annual mortality rates in adult-sized migrant Houbara Bustards (*Chlamydotis [undulata] macqueenii*). *Anim. Conserv.* 4: 133–141.

Cramp, S. (1980) *Handbook of the birds of Europe, the Middle East and North Africa: The birds of the Western Palearctic, Volume II hawks to bustards*. Oxford: Oxford University Press.

Dillingham, P. W. and Fletcher, D. (2008) Estimating the ability of birds to sustain additional human-caused mortalities using a simple decision rule and allometric relationships. *Biol. Conserv.* 141: 1783–192.

ESRI (Environmental Systems Research Institute) (1999) ArcView GIS version 3.2. ESRI, Redlands, California.

Herholdt, J. J. (1988) The distribution of Stanley's and Ludwig's Bustards in southern Africa: a review. *Ostrich* 59: 8–13.

Janss, G. F. E. (2000) Avian mortality from power lines: a morphologic approach of a species-specific mortality. *Biol. Conserv.* 95: 353–359.

Janss, G. F. E. and Ferrer, M. (2000) Common Crane and Great Bustard collision with power lines: collision rate and risk exposure. *Wildl. Soc. Bull.* 28: 675–680.

Jenkins, A. R., Smallie, J. J. and Diamond, M. (2010) South African perspectives on a global search for ways to prevent avian collisions with overhead lines. *Bird Conserv. Int.* 20: 263–278.

Martín, C. A., Alonso, J. C., Alonso, J. A., Palaćin, C., Magaña, M. and Martín, B. (2007) Sex-biased juvenile survival in a bird with extreme size dimorphism, the Great Bustard Otis tarda. *J. Avian Biol.* 38: 335–346.

Niel, C. and Lebreton, J-D. (2005) Using demographic invariants to detect overharvested bird populations from incomplete data. *Conserv. Biol.* 19: 826–835.

Raab, R., Spakovszky, P., Julius, E., Schutz, C. and Schuylze, C. H. (2011) Effect of power lines on flight behaviour of the West-Pannonian Great Bustard *Otis tarda* population. *Bird. Conserv. Int.* 21: 142–155.

Rollan, A., Real, J., Bosch, R., Tinto, A. and Hernandez-Matias, A. (2010) Modelling the risk of collision with power lines in Bonelli's Eagle *Hieraaetus fasciatus* and its conservation implications. *Bird Conserv. Int.* 20: 279–294.

Shaw, J. M., Jenkins, A. R., Smallie, J. J. and Ryan, P. G. (2010). Modelling power line collision risk in the Blue Crane *Anthropoides paradiseus* in South Africa. *Ibis* 152: 590–599.

Sundar, K. S. G. and Choudhury, B. C. (2005) Mortality of Sarus Cranes (*Grus antigone*) due to electricity wires in Uttar Pradesh, India. *Environ. Conserv.* 32: 260–269.

Tellería, J. L. (2009) Potential impacts of wind farms on migratory birds crossing Spain. *Bird Conserv. Int.* 19: 131–136.

Wade, P. R. (1998) Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Mar. Mamm. Sci.* 14: 1–37.

ANDREW R. JENKINS, JESSICA M. SHAW*, PETER G. RYAN
Percy FitzPatrick Institute, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa.

JON J. SMALLIE
Wildlife & Energy Programme, Endangered Wildlife Trust, Private Bag X11, Parkview 2122, South Africa.

BRADLEY GIBBONS
African Crane Conservation Programme, Endangered Wildlife Trust, Private Bag X11, Parkview 2122, South Africa.

RONELLE VISAGIE
Birds of Prey Programme, Endangered Wildlife Trust, Private Bag X11, Parkview 2122, South Africa.

**Author for correspondence; email: jessica.shaw@uct.ac.za*

Received 7 November 2009; revision accepted 22 December 2010;
Published online 8 July 2011