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Lek mating systems: a case study in the Little Bustard *Tetrax tetrax*

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Abstract

Leks have recently been defined as male display aggregations that females attend primarily for the purpose of mating. This is an extended version of previous definitions, as a clear-cut definition of leks is difficult to obtain. Four criteria should be verified to identify a lekking species: (i) there is no male parental investment beyond the sperm; (ii) males aggregate at specific sites for display; (iii) the only resource females find on the lek is the male, i.e. the male genes; (iv) females can select her mate(s), although the necessity of this latter condition for lekking species has been highly debated. We applied these criteria to the endangered little bustard *Tetrax tetrax*, a species that is claimed to show an exploded lek mating system, but for which this has never been fully investigated. We monitored a population of little bustards in western France during 2 years to investigate the two central criteria in the assessment of their mating system: male aggregation in arenas and lack of consistent resources in male territories. We analysed the spatial distribution of little bustard male territories, the individual variation in size, and the land use characteristics of male territories, with particular attention to the habitats that may be considered as defensible resources. Displaying males showed an aggregated spatial distribution over the study area during the 2 years of survey. Male territories were rather large (19 ± 16 ha), but a large among-male variability in territory size was observed. Land use within the territories included mainly permanent and semi-permanent crops. The variability in land use among territories suggests also that resources found within male territories were selected according to male needs (food and display) rather than to female needs (permanent crops that are more appropriate for reproduction). The mating system of the little bustard seems to match the general (and extended) definition of leks, at least in some populations. However, limits between resource defence polygyny and extreme exploded or resource-based leks are thin and unclear, and the little bustard is a good example of how lek definitions may be difficult to apply in non clear-cut empirical situations.

Keywords: Lek; Polygyny; Mating system; Little Bustard; *Tetrax tetrax*; Male territory

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1. Introduction

1.1. Bird mating systems

Mating systems in birds have received considerable attention since the major reviews of Lack (1968) or Emlen and Oring (1977), and more recently Davies (1991), Ligon (1999). Earlier classifications of bird mating systems were based on the number of mates (Lack, 1968), i.e. monogamy when one male mates with one female, polygyny when one male mates with two or more females and so on. A classification taking ecology and behaviour into account was then developed (Emlen and Oring, 1977). The discovery that social monogamy does not necessarily mean genetic monogamy, and the existence of extra-pair copulations as an alternative mating tactic changed our view of bird mating systems (Gowaty, 1985) and introduced flexibility and new parameters in theoretical models. The most recent classifications are now based on male and female patterns of dispersion, and on which parent gives parental care (Davies, 1991; Ligon, 1999 for a complete review).

Birds are very good models for studying mating systems, primarily because almost all types of mating systems have been described and well documented (see reviews in Davies, 1991; Ligon, 1999). Extreme cases include the strict monogamy in long-lived seabirds (Warham, 1990), promiscuity in Australian brush turkey (Jones et al., 1995), serial polyandry in phalaropes (Schamel and Tracy, 1977) or rheas (del Hoyo et al., 1992), simultaneous polyandry in Harris hawk (Bednarz, 1987), polygynandry in the alpine accentor (Davies et al., 1996), and various polygyny systems, including spectacular leks in forest grouses (Höglund and Alatalo, 1995). However, categorisation proves sometimes difficult, either between or even within species (e.g. Davies, 1991), or between categories (e.g. the frontier between resource defence polygyny, harem defence polygyny, lek polygyny or lek promiscuity: Emlen and Oring, 1977; Oring, 1982; Höglund and Alatalo, 1995; Ligon, 1999, and below).

From a conceptual point of view, the original mating system is promiscuity, from which monogamy, polyandry, polygyny and polygynandry can be defined through a reduction in randomness according to the number of individuals each member of each sex mates with (Lott, 1991). Phylogenetically, however, the original bird mating system may have been monogamy (with, or without bi-parental care), although other systems may have occurred first (see Wesolowski, 1994; Ligon, 1999). Polygyny, which is the rule in mammals, accounts for a small proportion of bird mating systems. However, amongst polygynous systems, a high diversity has been described in birds, factors of variation including mainly the amount and the type of resources that females get from males, from sperm only to some degree of parental care. The most extreme example of polygynous mating systems in birds is however the lek mating system.

Mating systems were formerly considered as being species-specific with little intra-specific variation, but recent studies have reported that some species show flexible mating patterns (review in Lott, 1991). Alternative male mating tactics sometimes co-occur within species (Lott, 1991; Davies, 1992; Gross, 1996), and that includes lekking (e.g. van Rhijn, 1973; Lank et al., 1995; Lanctot and Weatherhead, 1997).

1.2. Lekking in birds

The latest review of lekking in birds listed 98 species, i.e. less than 1% of all bird species, showing lek behaviour (Höglund and Alatalo, 1995). A more recent survey of the literature raises to 148 (i.e. 50% more) the number of bird species currently known to show lek behaviour (Appendix A), and this number is likely to increase, since mating systems are unknown in many bird species. Nevertheless, lekking species will remain an exception in birds, with a strong phylogenetic component (Höglund and Alatalo, 1995; Ligon, 1999). Lekking species have attracted interest among ecologists, ethologists and evolutionists because leks seem to offer ample opportunity for sexual selection and raise theoretical problems (e.g. the lek paradoxReynolds and Gross, 1990), as well as being impressive (Andersson, 1994).

Höglund and Alatalo (1995) proposed an extended definition of lek: a male display aggregation that females attend primarily for the purpose of mating. There is however no clear-cut definition of what identifies a lekking species, though it is generally agreed that these species are characterised by (i) the absence of male parental care, (ii) some degree of aggregation of displaying males, (iii) the fact that females do not find other resources than males (or their genes) on leks, and (iv) the fact that females can sample and select males (Bradbury, 1981; Oring, 1982; Höglund and Alatalo, 1995). However, the first character is shared by many non-lekking species (McKittrick, 1992). The second character is relative, not absolute (see Höglund and Alatalo, 1995, for discussing this point), and led to the recognition of dispersed leks (Gilliard, 1969) or exploded leks (Emlen and Oring, 1977). It is nonetheless an essential trait of lekking species (Beehler and Foster, 1988). The third character can also be discussed as a distinguishing criterion of lekking species, as pointed out by the existence of resource-based leks (Alexander, 1975). Finally, it has also been argued that the fourth character is not a discriminating criterion, as it may hold true for invertebrates, but not for vertebrates (Höglund and Alatalo, 1995). These remarks highlight the difficulties in finding a good definition of what constitutes lekking behaviour.

1.3. The bustards

The complexity around the definition of leks is especially well exemplified by the bustards (family Otididae). There are 25 species of bustards (five of which breed in the western Palearctic). In their review Höglund and Alatalo (1995) include only one species (the great bustard *Otis tarda*) as a lekking one. Data presented by Gaucher (1995) strongly suggest a lek mating system for the Houbara bustard *Chlamydotis undulata*, and actually, only one species (from genus *Eupodotis*) seems to be truly monogamous, although perhaps non-lekking mating system also holds for all three species of the genus and for the two *Lissotis* and the three *Heteropterax* species (del Hoyo et al., 1996). In the other 17 species of bustard, males do not provide any parental care, and according to Collar (in del Hoyo et al., 1996), most of these species are promiscuous and polygamous, and display communally (with displaying males clumped either in tightly associated territories or in groups of relatively dispersed territories). Additionally, female home ranges before laying largely oversize male territories in species that have been studied (Schulz, 1985; Osborne and Osborne, 1998; Alonso et al., 2000; Morales et al., 2000). Overall, the absence of a pair-bond, the pronounced sexual dimorphism as well as the existence of extravagant courtship displays all favour the hypothesis of lek mating system for most bustard species (del Hoyo et al., 1996). Discrepancy in the evaluation of bustard mating systems may originate in the fact that all species except the great bustard seem to show exploded leks, with distances between displaying males sometimes being particularly high. Additionally, there seems to be some degree of intra-specific variation in mating systems (Carranza et al., 1989, Collar in del Hoyo et al., 1996). Therefore, bustards seem to be a good model to study the variation in the relationship between male territory distribution or size, and mating system.

Surprisingly, the most common (although currently threatened) Palearctic species, the little bustard *Tetrax tetrax*, has seldom been investigated with respect to its mating system. It is generally agreed that it shows lekking behaviour, although in an exploded lek system: there is no male parental care in this species, males are clustered at display centres visited by females for mating, but they hold relatively large territories (Schulz, 1985). However, detailed information on patterns of spatial distribution of displaying males and on male territory characteristics is extremely scarce. Petretti (1993) suggested that males use an area of ca. 2 ha, but Schulz (1985) indicated that two radio-tracked males used an area of 27 and 83 ha (core areas of 5 and 9 ha respectively). Furthermore, the vegetation cover most frequently found around male display sites, i.e. permanent and semi-permanent cover (Martínez, 1994; Salamolard and Moreau, 1999) is also the vegetation cover that females apparently prefer (Salamolard and Moreau, 1999). Within a system where males hold territories of a few hectares in size, they may defend resources for themselves or for the females. Thus the frontier between the definition of the mating system as exploded (possibly resource-based) lek or as resource defence polygyny appears unclear. Such discrepancies highlight the importance of accurately describing male territorial behaviour in the species, including individual variability, and careful mapping of male territories (Bradbury, 1981) before attempting to analyse its mating system.

In this paper, we evaluate how the little bustard fits the lekking criteria. Of the four criteria specified above, the first, concerning the absence of male parental care, has been already proved (Schulz, 1985, personal observation). The fourth criterion, of free female choice, has been highly debated (see Höglund and Alatalo, 1995) and will not be considered here. The other two conditions, male aggregation in arenas and lack of resources for the females within male territories, are therefore central in the assessment of the mating system. We thus analyse the spatial distribution of little bustard male territories, the individual variation in size, and potential factors explaining this variability. We further analyse the land use characteristics of male territories, with particular attention to the habitats that may be considered as defensible resources from a female perspective. We finally discuss the implications of data presented to identify the mating system of this species.

2. Methods

The study area is located in the *Département des Deux Sèvres*, central western France (46°11′N, 0°28′W), and covers ca. 340 km^2 of intensive agricultural habitat. Land use in the study area is a mixture of winter cereal crops (ca. 35% of the surface), other winter crops such as rape-seed and peas (ca. 15%), spring-sown crops (sunflower and corn, ca. 25%), and pasture land and other permanent or semi-permanent crops directed to livestock rearing (ca. 15%).

Data used in this study were collected during April–July 1997–1998, although data of land-use characteristics within the territories includes data from the 1997 season only. The whole of the study area was checked regularly (at least once a week) by a team of three to eight people, to detect displaying males. Each area where males were sighted at least once was then monitored regularly (usually twice a week) throughout the study period. All little bustard observations were mapped, indicating date, sex, and exact position within fields. Males were identified according to plumage characteristics (Arroyo and Bretagnolle, 1999). Some observations in 1997 ($n = 15$, 2.5%) could not be assigned without doubt to a particular male, and were excluded from the analyses. Overall, 46 different males were monitored in 1997 and 55 in 1998. Mean (± S.D.) number of observations per male was 12.9 ± 11.9 (range 1–45) in 1997 and 16.0 ± 15.0 (range 1–67) in 1998. For the analysis of territory size, however, only males with at least ten observations were kept, in order to minimise the effect of the number of observation frequency on territory size (see below, and Table 1). Thus data set was reduced to 22 males in 1997 and 31 in 1998. Mean number of observations per male was then 23.2 ± 9.4 (range 11–45) in 1997 and 25.7 ± 13.8 (range 10–67) in 1998. Week of arrival and of departure (i.e. first and last week when a given male was identified without any doubt) were used to define length of stay (in weeks). Mean length of stay per male was 7.8 ± 4.8 weeks (range 1–17) for the 46 males, and 11.4 ± 3.6 weeks (range 4–17) for the sub-set of 22 males in 1997, and 6.3 ± 5.2 weeks (range 1–19) for the 56 males and 9.4 ± 4.8 weeks (range 2–19) for the sub-set of 31 males in 1998.

Observations were plotted on a digitalised map of the study area using a Geographical Information System (ARCVIEW 3.b software, Environmental Systems Research Institute Inc., 1996). Territories were modelled using the Ranges V package (Kenward and Hodder, 1996), using the core-weighting kernel method as an estimator (Worton, 1989; Boulanger and White, 1990; Worton, 1995). Four other non-parametric estimators were also tested, but the core-weighting kernel method provided the most robust results with regard to the variation in the number of observations per individual (Table 1). Furthermore, the core-weighting kernel method minimised the influence of isolated points to the total territory size (Fig. 1). This is important in the case of the little

Table 1
Spearman rank coefficients of correlation (r_s) between territory size and number of observations for each of the non-parametric home-range estimating methods[a]

		Estimating method									
	n	Fixed		Kernel core-weighting		Tail-weighting		Minimum convex polygon		Harmonic mean	
		r_s	P	r_s	P	r_s	P	r_s	P	r_s	P
Core	22	0.332	n.s.	0.441	n.s.	0.310	n.s.	0.451	0.03	0.763	<0.001
Total	22	0.524	0.01	0.545	0.009	0.708	<0.001	0.607	0.003	0.802	<0.001

[a] n is the number of territories.

bustard, as they probably do not relate much to their main range, but rather to occasional movements. Core ranges were determined using the utilisation plot graph given by the home-range software program, slope discontinuities being used as indicators of core (Kenward, 1987).

Territory baricenter for all males (including those with less than ten observation points) was plotted back on the digitalised map to evaluate male spatial distribution within the study area. Spatial distribution was tested with the distance to the nearest neighbour method (Clark and Evans, 1954; Krebs, 1989). The expected distance to the nearest neighbour in a population with a random spatial pattern is defined by $r_E = 1/2\sqrt{\rho}$ (where ρ is the density). The ratio R between the observed (r_A) and the expected distance to the nearest neighbour provides an index of aggregation of individuals: R values lower than 1 indicate increasing levels of clumping. The two-tailed significance of the deviation from randomness was tested from the standard normal deviate $z = (r_A - r_E)/s_r$, where $s_r = 0.26136/\sqrt{n\rho}$ is the S.E. of the expected distance to the nearest neighbour (Krebs, 1989). The random distribution of permanent grassland covers was tested using the Quadrat operation of the IDRISI package. Quadrats are cellular divisions of the area. The quadrat module determines the variance/mean ratio of points in cases. The variance/mean ratio is a technique used to describe the pattern of a point set, ranging from random (values lower or close to 1.0) to clustered (values greater than 1.0) distribution (Ludwig and Reynolds, 1988).

Total territory surface (100% home-range) for the 22 males in 1997 was mapped back on the digitalised map using the GIS, to calculate the percentage of each crop type in each territory, and

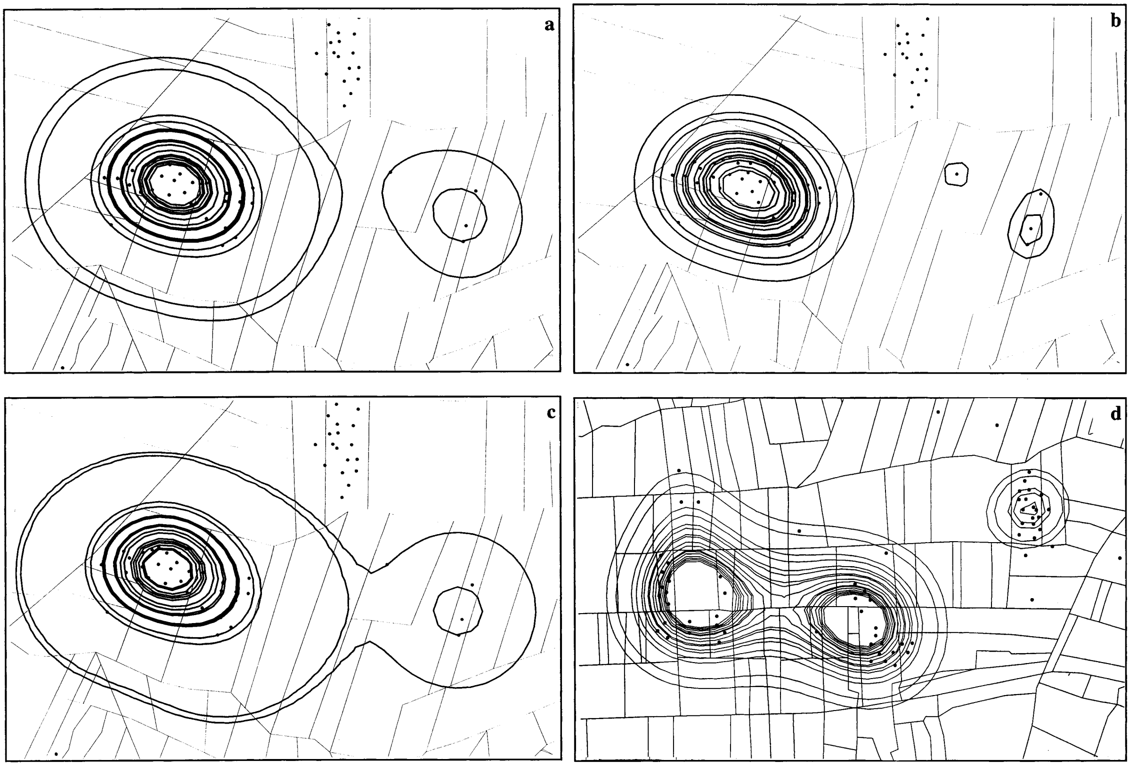

Fig. 1. Territory of a typical individual little bustard male, calculated with (a) fixed kernel, (b) core-weighting kernel and (c) kernel with optimised smoothing parameter estimating methods; (d) territory of another male (core-weighting kernel estimator). Isopleths are shown for each territory (isolines of equal fix density).

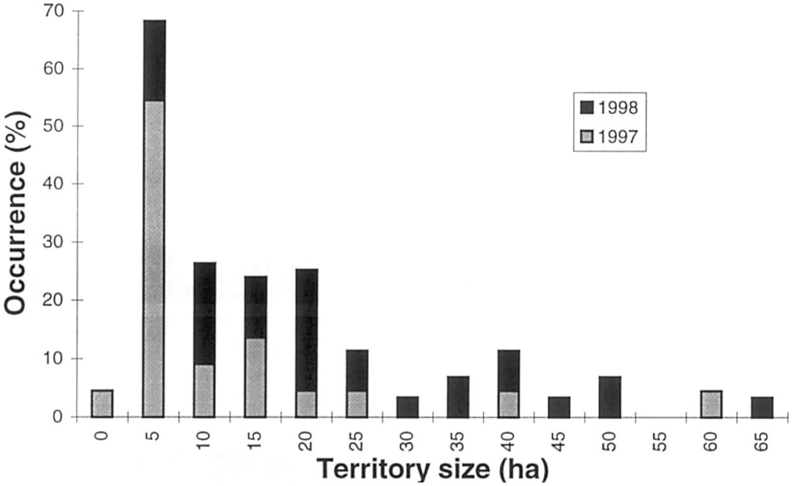

Fig. 2. Frequency distribution of male little bustard total territory size (outliers are excluded: see Section 3).

compare it to land use of the complete study area. Crop types were arbitrarily classified into eight categories: winter cereals (wheat and barley), rape-seed, corn, sunflower, ray-grass, ploughed fields, fields with permanent or semi-permanent covers (pasture land, alfalfa, fallow land or set-aside fields), and low-height annual crops (peas and flax). Cereal and rape-seed crops provide neither food nor display conditions for males. Permanent crops, sunflower and ray-grass fields provide both visibility and food. Ploughed fields, corn crops and low-height annual crops provide good visibility, but only the latter provide occasional food. Between-territory variation in land use was summarised using a principal component analysis (PCA) performed on the eight land use variables (% of each crop type on the territory).

3. Results

3.1. Size and distribution of male territories

Males were not randomly distributed within the study area: their locations were significantly clumped in both years of the study (Fig. 2, Table 2). Eight males (17%) in 1997 and 11 (20%) in 1998 were observed just once or twice during the same week, and then disappeared. These males were mostly observed in isolated locations. When excluding these males from the analysis, spatial distribution of resident males was still significantly clumped (Table 2).

Clumped male distribution was apparently not due to lack of suitable habitat in the areas where little bustard males were absent, nor to a clumped distribution of favourable habitats, at least when assuming that favourable habitats were permanent or semi-permanent crops. These habitats were present in 95% of 296 quadrates of 1 km^2 (covering the whole study area and with at least half the surface with known referenced cover), far more than the 15% that little bustard males occupied. Moreover, the distribution of these habitats within our study area was not clumped, as suggested by the coefficient of dispersion (CD), σ^2/μ (CD = 0.998, $P > 0.05$; data from 1998). However, we cannot exclude the hypothesis that some parameters related to habitat quality affected male distribution, as the proportion of grassland habitat in grid cells occupied or not by males in 1998, revealed that grassland habitat availability was slightly higher in grid cells where males settled (15.9 ± 11.0 vs. 12.2 ± 11.2%; $F_1 = 4.18$, $P = 0.042$).

Mean total territory size for the 53 males was 46.0 ± 140.2 ha (range 0.7–763). The large S.D. arose, mainly, due to two males in 1998 having atypical territories, and behaving as outliers. Territory size for these males was 722 and 763 ha

(100.5 and 138.2 ha for core territories). These two males occupied each two and three different display areas throughout the season, each of these sub-territories separated by more than 1 km. These sub-territories were separated when considering the 95% fixes isopleth of core-weighting kernel models. These males were considered satellites, to differentiate them from the other males, called residents. Another male in 1997 had a territory with three different cores, and its territory was the largest recorded that year (62.2 ha). However, this male was not considered as a satellite, given that its territory size was within the range of the rest of the population. Mean territory size excluding satellites was 18.7 ± 16.2 ha (0.7–66.6). The size of each of the sub-territories of the satellite males was 13.9 ± 4.6 (9.5–20.4, $n = 5$), not significantly different than those of resident males (median 14.0 ha, Mann–Whitney test, $W = 139$, $P = 0.9$). Mean core territory size was 13.5 ± 22.7 ha (0.7–138), or 9.3 ± 7.4 ha (0.7–35.2) excluding the satellites. All subsequent analyses refer only to total home range.

Territory size within the resident population was not normally distributed (Fig. 3; Shapiro–Wilk test, $W = 0.850$, $P < 0.0001$; see Shapiro and Wilk, 1965): most individuals held relatively small territories, whereas only a small proportion of the population held increasingly larger territories. Overall, there existed a large variability in territory sizes. Territory size was significantly larger in 1998 (median 18.4 ha, excluding the satellites) than in 1997 (median 6.7 ha, Mann–Whitney test, $W = 409$, $P = 0.002$). Additionally, among-male variability in territory size each year was also important, even excluding the satellite males (Fig. 3). Variability in territory size was not related to the number of neighbouring males within a kilometre ($r = -0.256$, $n = 22$, $P > 0.2$ in 1997 and $r = -0.115$, $n = 29$, $P > 0.5$ in 1998) nor to arrival time ($r = -0.089$, $n = 22$, $P > 0.5$ in 1997, $r = -0.124$, $n = 29$, $P > 0.5$ in 1998). Variability in territory size was however significantly related to length of stay in 1998 ($r = 0.478$, $n = 29$, $P < 0.01$), but not in 1997 ($r = 0.171$, $n = 22$, $P > 0.3$).

3.2. Land use in bustard territories

A principal component analysis was performed on the 22 territories in 1997, using the proportion of each of the eight crop types in the territory as explanatory variables. Only the first four axes were significant (Eigen values above 1), and explained ca. 80% of the total variance (Table 3). PC1 was positively correlated with the proportion of cereals, oilseed rape and ploughed fields; PC2 was positively correlated with the percentage of sunflower and ray-grass, and negatively with the percentage of permanent crops; PC3 was positively correlated with the percentage of corn and ray-grass; PC4 was positively correlated with the percentage of low height annual crops (peas and flax). The first two axis were considered to be the most biologically meaningful, as they were related

Table 2
Test values (two-tailed) for aggregation in the spatial distribution of males within the study area[a]

	1997		1998	
	All males	Long stayers only	All males	Long stayers only
n	46	38	55	44
ρ	0.135	0.112	0.162	0.129
r_A	0.929	0.938	0.941	0.903
r_E	1.359	1.496	1.243	1.390
R	0.683	0.627	0.757	0.649
z	−4.107	−4.394	−3.451	−4.448
P	0.0001	0.0001	0.001	0.0001

[a] n is the number of males; ρ is the density; r_A is the average observed distance to the nearest neighbour; $r_E = 1/2\sqrt{\rho}$ expected distance to the nearest neighbour in a random pattern; $R = r_A/r_E$, the index of aggregation; $z = (r_A - r_E)/s_r$, where $s_r = 0.26136/\sqrt{n\rho}$; P is the significance value of departure from a random pattern.

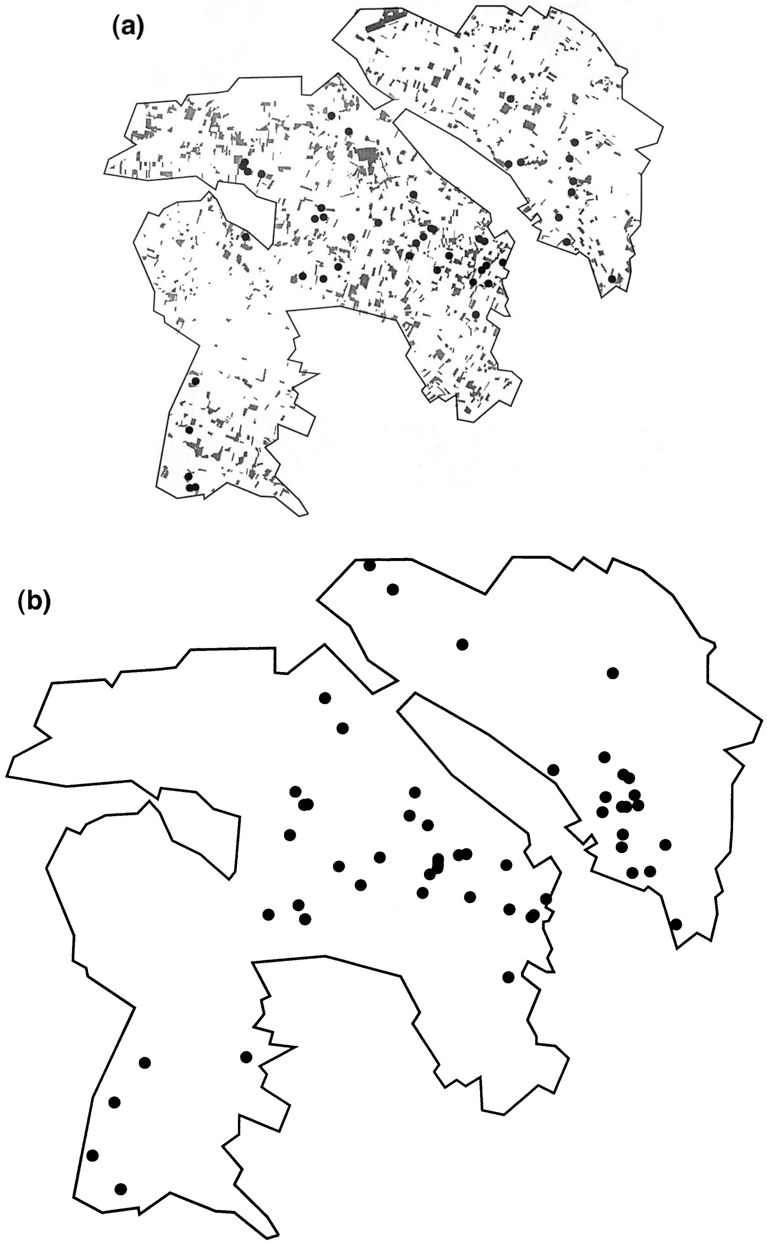

Fig. 3. Distribution of male territories in 1997 (a) and 1998 (b) within the study area. Each black dot represents the centre of a given male territory. Grey shades superimposed on (a) represent grassland habitats (ray-grass and permanent crops) available in 1997.

to the most positive (PC2) and negative (PC1) crops for the bustards in terms of display cover and food supply.

Territories were not uniformly distributed along PC1 axis: most had negative loadings (Fig. 4), which indicates that most territories were characterised by a low proportion of cereal and oil seed rape, despite their overall abundance (Table 4). Overall, ca. 70% of the male territories were covered by sunflower, ray-grass or permanent crops,

Table 3
Correlation matrix of the land-use variables and the first four axes of the principal component analysis performed for the 22 little bustard territories in 1997 (significant correlations are in italics)

	PC1	PC2	PC3	PC4
Eigenvalues	2.126	1.766	1.288	1.175
% Variance	26.6	22.1	16.1	14.7
Cumulative %	26.6	48.7	64.7	79.4
Variable				
Cereals	*−0.564*	0.090	−0.183	−0.042
Corn	0.063	−0.392	*0.660*	0.068
Sunflower	−0.281	*0.501*	0.008	−0.294
Oil-seed rape	*0.504*	0.059	−0.336	−0.235
Peas/flax	0.011	0.006	−0.208	*0.877*
Permanent crops	−0.311	*−0.566*	−0.231	−0.275
Ray grass	−0.008	*0.482*	*0.456*	0.035
Ploughed fields	*0.498*	−0.176	0.336	−0.079

which represented thus the most important land cover within territories (Table 4). In contrast, the distribution of territories along PC2 was rather regular (Fig. 4): territories ranged thus between those with a high percentage of permanent crops, but low percentage of ray-grass and sunflower, to those with high percentage of ray-grass and sunflower to detriment of permanent crops.

Territory size was positively correlated with PC1 ($r = 0.584$, $n = 22$, $P < 0.005$), but not with PC2 ($r = 0.110$, $n = 22$, $P > 0.2$). However, territory size was strongly correlated with the total surface of permanent crops and ray-grass inside the territory ($r = 0.917$, $n = 22$, $P < 0.0001$), but not with the total surface of sunflower ($r = 0.241$, $n = 22$, $P > 0.5$).

4. Discussion

4.1. Territory size in little bustard: comparison with previous estimates

Average territory size found in this study was 19 ha, an intermediate value between those reported by Petretti (1993); 2 ha and Schulz (1985), 27–83 ha. These differences may arise from observation, sampling or estimating methods. Petretti (1993) based his results on field locations recorded during 2 consecutive days per male and season, thus excluding variations that may occur throughout the season or according to temporal activities

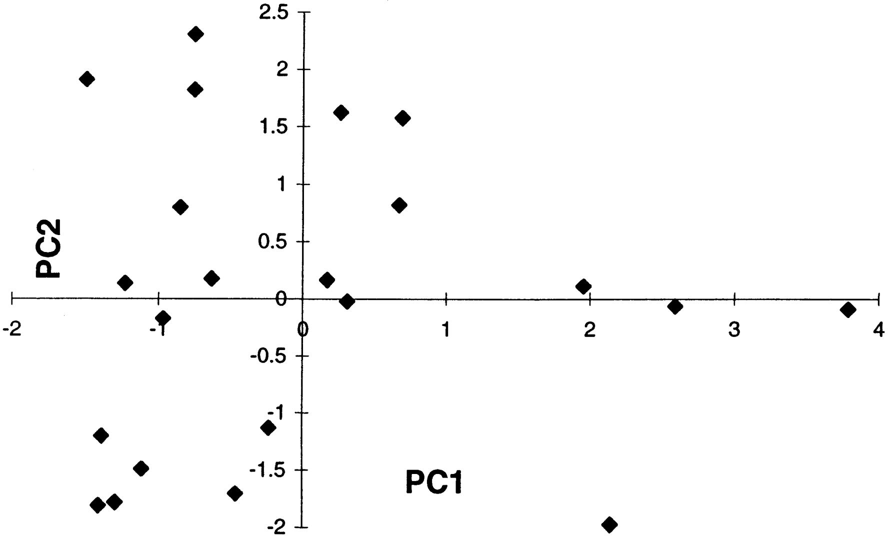

Fig. 4. Distribution of values of PC1 and PC2 (first two axes of the principal component analysis of land use variables) of male little bustard territories. See Table 3 for the interpretation of axis.

Table 4
Average (mean, S.D., range and coefficient of variation) percentages of crop types in male little bustard territories ($n = 22$), compared to that available over the total study area (34 000 ha)[a]

	Cereals + oil-seed rape (no food, no cover)	Sunflower + ray-grass + permanent crops (food and cover)	Peas + flax (cover, occasional food)	Corn + ploughed fields (cover, no food)
Availability in study area (%)	53	33	4	10
Bustard territories (%)				
Mean	21	69	4	6
S.D.	22	29	18	13
Range	0–68	0–100	0–86	0–49
CV	102	42	417	222

[a] Crop types are grouped according to their importance in terms of food and display cover for males.

(display, feeding, etc.). His values probably refer to a core area or display site rather than home range. Estimates of male territories from the two radio-tracked males in Portugal (Schulz, 1985) were obtained using the minimum convex polygon method. This method directly binds isolated plots to the core territory, and thus over-estimates the territory size when compared with the method we chose.

Additionally, these differences in territory size may arise from variation in ecological variables, such as bird density or habitat availability, as has been found in other bird species, even lekking ones (e.g. ruffed grouse *Bonasia umbellus*: Thompson and Fritzell, 1989, black grouse *Tetrao tetrix*: Höglund and Stöhr, 1997). Male density is expected to limit the maximum size of territories. Foster (1983) suggested that disturbance by other males may influence the distribution of display sites. In populations with low breeding density, territory holders would experience a reduced intruder pressure, allowing the size of the defended space to expand. An expanded defended space could eventually include enough resources to cross the categorical threshold from classical lek to exploded lek, or even territorial polygyny. However, density did not seem to explain variations in territory size for little bustards from different locations. Overall density of displaying males in our study area was 0.13/100 ha, reaching locally up to 0.30/100 ha. In some areas in Portugal male density reaches 47 displaying males/100 ha (Moreira and Leitão, 1996), and mean territory size must thus be far less than the 19 ha as found in our study, unless territories largely overlap. Furthermore, territory size changed significantly among years in our study area, whereas bustard density remained relatively constant. Additionally, a large individual variation in territory size in our study area was noted, which was apparently not related to variations in local density. Therefore, other variables may be also involved in explaining among site, among male or among-year variability in territory size, probably involving to some degree the habitat availability.

4.2. Land use in male territories: resources for males or females?

Habitat availability may affect territory size, as a male may have to defend a larger area to include preferred suitable crops. In the capercaillie *Tetrao urogallus*, a species with exploded leks, home range size is inversely related to availability of bilberry and late stage forests (Storch, 1995). Land use within male little bustard territories was diversified, possibly because males must simultaneously find food, good cover for display, and good sound transmission conditions (Salamolard and Moreau, 1999). Our results confirmed that land use within male territories reflected the balance between food and display cover. Cereal and rape-seed crops are too high in spring to allow visibility of displaying males, and they provide no food once the plants are fully grown. These crops were avoided, except in very large territories. This was expected as $>50\%$ of the study area is covered by cereal and rape-seed crops. Thus, if small territories might include only preferred habitat (grassland cover), the proportion of cereal and rape-seed crops necessarily increases as territory size increases. In contrast, all crops highlighted by PC2 axis provide both appropriate cover (visibility in those crops is high until early summer) and food, and are present in male territories more frequently than expected from their availability (Martínez, 1994; Salamolard and Moreau, 1999, this study).

Although use of the male territory by females is not thought to be a critical aspect of exploded lek systems, females can potentially forage and nest within male's territory, conversely to true leks (Höglund and Alatalo, 1995). It has been argued that systems in which external resources affect female choice should be treated together with mating systems where male resources are essential, i.e. resource defence polygyny (Höglund and Alatalo, 1995). However, it should be noted that it is not the absence of resources within territories that should distinguish lekking from non-lekking species, but the degree to which males regulate female access to those resources in order to obtain mating (Bradbury, 1985). It appears therefore of critical importance to evaluate how males control female access to resources in species with presumed exploded lek mating system.

Suitable crops differ in quality for male and female little bustards. Permanent crops hold diverse and abundant food (Martínez, 1994) and might be very important for female reproduction (Panek, 1997). Crops such as sunflower and ray-grass form also part of male and female diet; little bustard nests have been occasionally found in ray-grass fields, but never in sunflower crops. Therefore, permanent crops and ray-grass/sunflower have a very different value for female breeding, whereas its differential value in terms of food and cover for males is less marked. Male territories contained a high and rather constant proportion of good food and cover crops (ray-grass, sunflower and permanent crops, Table 4). However, territories varied in relation to which of the preferred feeding crops were present in the territory: permanent crops or ray-grass/sunflower. This suggests that resources found within male territories were more likely selected according to male needs (a high proportion of food and display cover, regardless of the source) than to female needs (permanent crops for reproduction). Nonetheless, territory size was significantly and positively related to the total surface of permanent crops and ray-grass (potentially nesting habitats), but not to sunflower (which provides food for males but not nesting habitat for females). This latter result may suggest that some males defend large territories to assure a better availability of the female's preferred habitat for nesting.

4.3. Does male territory distribution and characteristics support a lek mating system in little bustard?

Male little bustards do not provide parental care (Schulz, 1985; personal observation), thus fulfilling the first criteria of lekking species (Höglund and Alatalo, 1995). An aggregation of displaying males (second criterion) is an essential trait of lekking species (Beehler and Foster, 1988). Little bustard males in our study area were significantly aggregated, although their territories were very large. Habitat constraints may explain partly a clumped male distribution, e.g. males may be clumped in areas where their preferred crops are more abundant. However, the critical question is whether there is aggregation within the habitat used by the species, or whether the species is closer to solitary along the continuum from clumped to solitary display (Höglund and Alatalo, 1995). If habitat limitations explain male clustering, but males distribute uniformly within the available habitat, we are not dealing with a lek but with landmark aggregations (Höglund and Alatalo, 1995). For instance, many bowerbirds were first considered to be lekking, but are now known to defend solitary display sites, with male territories being regularly distributed along suitable ridges of montane forest (Pruett-Jones and Pruett-Jones, 1982; see also Appendix A). Distribution of permanent grassland crops in our study area was relatively homogeneous and did not differ statistically from random distribution (Fig. 2). Little bustard males were also absent from many areas with abundant permanent crops. Therefore, landmark aggregation in this species appears unlikely. However, even if habitat characteristics alone do not explain the clumped distribution of males, a more detailed analysis of the influence of habitat quality and resource availability on male distribution would help confirm this point.

The third criterion identifying lekking species (females find no other resource than males on leks) could not be established firmly from our data. Leks, as opposed to other mating systems based on promiscuity and male dominance, occur when female home ranges are large and overlapping (Oring, 1982). Schulz (1985) found home ranges of 589 and 1206 ha for two females in Portugal before they laid eggs. These home ranges are far greater than male territory sizes, and also support a lek mating system. But little bustard males could be considered to display on resource-based leks (Alexander, 1975), similarly to some hummingbirds in which grouped males display close to particular nectar flowers that females feed on (Stiles and Wolf, 1979). Permanent crops are also important for males in terms of food, so they may be present in the territories as an advantage for the males, which have to display and feed in their territories throughout the season. Furthermore, if female little bustards have been found breeding far away from male territories (> 1 km: Schulz, 1985, unpublished data), which supports a lek mating system, nests within male territories have also been found (unpublished data), in support of a resource defence polygyny mating system. The frontier between lek and resource defence polygyny is further weakened by the fact that some males may switch from one system to the other, within a breeding season. Temporary attendance of leks has already been described in other birds (Cartar and Lyon, 1988; Lanctot and Weatherhead, 1997). Similarly, the degree of aggregation of male little bustards is variable: if males were aggregated in the two years of our study, a random distribution has been found in other areas of western France (unpublished data), as is the case in the black grouse (Höglund and Stöhr, 1997). Some little bustard populations may thus show a dispersed polygyny mating system, in which males provide no parental care, but are not clustered on leks (Höglund and Stöhr, 1997), while other populations are more typically lekking. Experimental tests on lekking in this species may help in the future to determine, for a given population, which is the process leading to the formation of male aggregations, and which kind of lek mating system is operating (see Jiguet et al., 1998).

4.4. Conclusion

The mating system of the little bustard matches the general (and extended) definition of leks, as given by Höglund and Alatalo (1995), although this may not hold true in some populations. Actually, the limits between resource defence polygyny and resource-based or exploded leks can be thin, with a continuum from typical to intermediate species. Factors such as density, sex-ratio or habitat quality may influence mating systems in the little bustard, as has been found for other birds (see review in Lott, 1991; Byrkjedal et al., 1997), including lekking ones (Cartar and Lyon, 1988; see Table 1) and even another species from *Otididae* (Carranza et al., 1989). Variability in bird mating systems has also been found within populations (see Lott, 1991; Parish et al., 1997). The little bustard is therefore an example of how lek definitions may be difficult to apply in non clear-cut empirical situations. Intra-specific variation in mating system is however of profound importance when trying to understand the ecological and evolutionary factors that cause differences between mating systems (Lott, 1991). It is also essential to appreciate the mating system variability and flexibility of this endangered species in order to elaborate pertinent conservation measures (Jiguet et al., 1998).

More generally, data in Appendix A for bird leks suggest that exploded and/or resource-based leks are quite common (at least 39% of species considered, compared to 37% showing true lek behaviour), and that within-species variation in mating systems is also frequent (18% of lekking species with at least some populations not lekking). Previous studies of lek mating systems have focused on typical lekking species, such as ruff *Philomachus pugnax*, black grouse, sage grouse *Centrocercus urophasianus* or great snipe *Gallinago media*. Many of these detailed studies indicated that spatial, morphological and behavioural traits can be related to male mating success (Höglund and Alatalo, 1995). Much is known about female choice and correlates of male mating success in true lekking species, but very few studies have investigated in detail the pertinence of the same models in exploded or resource-based leks. Furthermore, exploded or resource-based lek species are more inclined to show intra-specific variations in their mating system (see Appendix A), probably due to variation in resource availability among populations. Detailed studies on the mechanisms implied in male aggregations in such species should allow to understand the processes associated to those variations.

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Appendix A

A list of bird taxa showing lekking behaviour. Source is Höglund and Alatalo (1995), except when specified. When information was available, we have differentiated species showing classical true leks, exploded or resource-based leks. Resource-based leks are probably commoner in hummingbirds than illustrated here. Additionally, we have indicated whether intra-specific variations in mating system (mixed) have been described (i.e. some populations have been described to lek, while others do not). The question mark indicates species probably not lekking, according to Höglund and Alatalo (1995).

Taxa	*Lek type*				Source
	True lek	Exploded lek	Resource based lek	Non-lekking populations	
Galliformes					
Phasianidae					
Tetraoninae					
Falcipennis falcipennis Siberian Grouse		+			(1)
Falcipennis canadensis Spruce Grouse		+			(1)
Centrocercus urophasianus Sage Grouse	+				
Dendragapus obscurus Blue Grouse		+		*	
Tetrao urogallus Capercaillie		+			
T. parvirostris Black-billed Capercaillie		+			
T. tetrix Black Grouse	+			*	
T. mlokosiewiczi Caucasian Black Grouse	+				
Tympanuchus cupido Greater Prairie Chicken	+				
T. pallidicinctus Lesser Prairie Chicken	+				
T. phasianellus Sharp-tailed Grouse	+				
Phasianinae					
Argusianus argus Great Argus		+			
Rheinardia ocellata Crested Argus		+			(1)
Pavo cristatus Indian Peafowl	+				
Pavo muticus Green Peafowl	+				(1)
Meleagrinae					
Meleagris gallopavo Turkey				*	
Gruiformes					
Otididae					
Tetrax tetrax Little Bustard		+			(2)
Neotis denhami Denham's Bustard		+			(3)
N. ludwigii Ludwig's Bustard		+			(3)
N. heuglinii Heuglin's Bustard		+			(3)
N. nuba Nubian Bustard		+			(3)
Chlamydotis undulata Houbara Bustard		+			(3)
Ardeotis kori Kori Bustard		+			(3)
A. nigriceps Great Indian Bustard		+			(3)
A. australis Australian Bustard		+			(3)
Otis tarda Great Bustard		+		*	
Lophotis ruficrista Red-crested Bustard		+			(4)
L. savilei Savile's Bustard		+			(3)
L. gindiana Buff-crested Bustard		+			(3)
Afrotis afra Black Bustard		+			(4)
A. afraoides White-quilled Bustard		+			(3)
Houbaropsis bengalensis Bengal Florican		+			(3)
Sypheotides indica Lesser Florican		+			(3)
Charadriiformes					
Scolopacidae					
Philomachus pugnax Ruff	+				
Tryngites subruficollis Buff-breasted Sandpiper	+			*	

		Gallinago media Great Snipe	+				
Psittaciformes							
	Psittacidae						
		Strigops habroptilus Kakapo	+				
Apodiformes							
	Trochilidae						
		Glaucis hirsuta Rufous-breasted Hermit				*	
		Threnetes ruckeri Band-tailed Barbthroat		+			
		T. leucurus Pale-tailed Barbthroat		+			(5)
		Eutoxeres aquila White-tipped Sicklebill					
		Phaethornis ruber Reddish Hermit					
		P. yaruqui White-whiskered Hermit	+				(5)
		P. guy Green Hermit	+			*	
		P. syrmatophorus Tawny-bellied Hermit	+				(5)
		P. superciliosus Long-tailed Hermit			+		
		P. boursieri Straight-billed Hermit	+				(5)
		P. squalidus Dusky-throated Hermit	+				(5)
		P. malaris Great-billed Hermit					(6)
		P. longuemareus Little Hermit	+				
		Androdon aequatorialis Tooth-billed Hummingbird	+				(7)
		Campylopterus cuvierii Scaly-breasted Hummingb.		+			
		C. hemileucurus Violet Sabrewing	+				
		C. largipennis Gray-breasted Sabrewing		+		*	(5)
		C. rufus Rufous Sabrewing			+		(8)
		Colibri delphinae Brown Violet-ear		+			(5)
		C. thalassinus Green Violet-ear		+		*	(5)
		Topaza pella Crimson Topaz			+		
		Klais guimeti Violet-headed Hummingbird	+			*	
		Eupherusa nigriventris Black-bellied Hummingbird				*	(6)
		Hylocharis eliciae Blue-throated Goldentail	+				(6)
		Chrysuronia oenone Golden-tailed Sapphire				*	(6)
		Amazilia tzacatl Rufous-tailed Hummingbird			+		(7)
		Agyrtria candida White-bellied Emerald					(9)
		Polyerata amabilis Blue-chested Hummingbird		+			
		Microchera albocoronata Snowcap	+				(6)
		Anthocephala floriceps Blossomcrown	+				(5)
		Heliodoxa jacula Green-fronted Brilliant			+		(7)
		Calliphlox brynatae Magenta-throated Woodstar					(6)
		Calypte anna Anna's Hummingbird			+		
		Selasphorus platycercus Broad-tailed Hummingbird			+		
Coraciiformes							
	Trogonidae						
		Trogon melanocephalus Black-headed Trogon	+				(8)
		Trogon citreolus Citreoline Trogon	+				(8)
Piciformes							
	Indicatoridae						
		Indicator indicator Black-throated Honeyguide				*?	
		I. minor Lesser Honeyguide				*?	
		I. variegatus Scaly-throated Honeyguide				*?	
Passeriformes							
	Tyrannidae						
		Mionectes oleagineus Ochre-bellied Flycatcher		+			
		M. macconnelli McConnell's Flycatcher		+			
		M. rufiventris Grey-hooded Flycatcher		+		*	
	Pipridae						
		Machaeropterus regulus Striped Manakin		+			
		M. pyrocephalus Fiery-capped Manakin		+			
		M. deliciosus Club-winged Manakin		+		*	
		Pipra pipra White-crowned Manakin		+			(10)
		P. rubrocapilla Red-headed Manakin		+			(10)

	P. aureola Crimson-hooded Manakin	+			
	P. fasciicauda Band-tailed Manakin	+			
	P. erythrocephala Golden-headed Manakin		+		
	P. mentalis Red-capped Manakin		+		
	P. coronata Blue-crowned Manakin			*	
	P. cornuta Scarlet-horned Manakin				(11)
	P. chloromeros Round-tailed Manakin				
	P. filicauda Wire-tailed Manakin	+			
	Manacus manacus White-bearded Manakin	+			
	M. vitellinus Golden-collared Manakin	+			
	M. candei White-collared Manakin	+			(8)
	Chiroxiphia caudata Swallow-tailed Manakin	+			
	C. pareola Blue-backed Manakin	+			
	C. linearis Long-tailed Manakin	+			
	Corapipo gutturalis White-throated Manakin	+			
	C. leucorrhoa White-ruffed Manakin				
	Ilicura militaris Pin-tailed Manakin		+		
Cotingidae					
	Cotinga maynana Plum-throated Cotinga				
	Lipaugus unirufus Rufous Piha	+			
	L. vociferans Screaming Piha	+			
	L. fuscocinereus Dusky Piha	+			
	Pyroderus scutatus Red-ruffed Fruit Crow	+			
	Rupicola rupicola Guianian Cock-of-the-Rock	+			
	R. peruviana Andean Cock-of-the-Rock	+			
	Phoenicercus carniflex Guianian Red Cotinga	+			
	P. nigricollis Black-necked Red Cotinga	+			
	Procnias tricarunculata Three-wattled Bellbird				
	P. alba White Bellbird				
	P. averano Bearded Bellbird				
	P. nudicollis Bare-throated Bellbird	+			
	Cephalopterus glabricollis Bare-necked Umbrella B.				
	C. ornatus Amazonian Umbrella Bird	+			
	C. penduliger Long-wattled Umbrella Bird			*	
	Perissocephalus tricolor Capuchinbird	+			
	Tijuca atra Black-and-gold Cotinga				
Oxyruncidae					
	Oxyruncus cristatus Sharpbill		+		
Philepittidae					
	Philepitta castanea Velvet Asity		+		(12)
Pycnonotidae					
	Pycnonotus latirostris Yellow-whiskered Greenbul				
Ploceidae					
	Euplectes jacksoni Jackson's Widowbird		+		
	Vidua macroura Pin-tailed Whydah				
	V. paradisaea Paradise Whydah			*	
	V. orientalis Broad-tailed Paradise Whydah				
	V. orientalis obtusa Angolan Paradise Whydah				
	V. chalybeata Village Indigobird		+		
Ptilonorhynchidae					
	Ptilonorhynchus violaceus Satin Bowerbird			*?	
	Prionodura newtoniana Newton's Golden Bowerb.			*?	
	Scenopoeetes dentirostris Tooth-billed Catbird	?			
	Amblyornis macgregoriae MacGregor's Bowerbird			*?	
Paradisaeidae					
	Semioptera wallacei Wallace's Standardwing	+			
	Cicinnurus regius King Bird of Paradise		+		
	Pteridophora alberti King of Saxony Bird of Parad.			*	
	Paradisaea raggiana Raggiana Bird of Paradise	+			
	P. apoda Greater Bird of Paradise	+			

P. minor Lesser Bird of Paradise		+				
P. rubra Red Bird of Paradise		+				
P. guilielmi Emperor of Germany Bird of Paradise		+				
P. decora Goldie's Bird of Paradise		+				
Astrapia sefilata Arfak Astrapia						
A. splendidissima Splendid Astratia			+		*	(13)
A. mayeri Ribbon-tailed Astrapia					*	(13)
A. stephaniae Stephanie's Astrapia		+				(13)
Parotia carolae Queen Carola's Parotia			+			
P. lawesii Lawe's Parotia			+			
P. wahnesi Wahne's Parotia			+			
Total number of species	148	55	51	7	26	

Sources : (1) del Hoyo et al., 1994; (2) Schulz, 1985; (3) del Hoyo et al., 1996; (4) Urban et al., 1986; (5) Hilty and Brown, 1986; (6) del Hoyo et al., 1999; (7) Bleiweiss, 1998; (8) Howell and Webb, 1995; (9) Atwood et al., 1990; (10) Castro Astor et al., 1998; (11) Ridgely and Tudor, 1994; (12) Prum and Razafindratsita, 1997; (13) Frith and Beehler, 1998

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