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EXPLODED LEKS: WHAT BUSTARDS CAN TEACH US

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SUMMARY.—*Exploded leks: what bustards can teach us.* In lek mating systems, males defend small, clustered courts visited by females to mate (Höglund & Alatalo, 1995). Lekking species should meet four criteria proposed by Bradbury (1981): (1) there is no male parental care, so that males contribute nothing to the next generation apart from gametes; (2) males aggregate at specific sites for display; (3) the only resource females find at the lek are the males themselves, that is, male genes; (4) females can select their mate(s). However, many studies have shown the existence of mating systems that do not fit completely these conditions but that still should be considered as leks. Exploded leks (Gilliard, 1969; Emlen & Oring, 1977) form one of the main categories of such «non-classical» leks. In exploded leks, males displaying in the assemblage are considerably separated and aggregation is not detectable until they are mapped over a large area (Bradbury, 1981). As a consequence, males hold larger territories, and females can forage and even nest within them (Ligon, 1999), thus apparently failing to meet Bradbury's third condition. Here, a review of some of the main issues related to exploded leks in birds are presented, emphasising the relevance of exploded leks in the study of lek evolution and female choice, given their features intermediate between classical leks and resource-based polygyny. The family of bustards, *Otididae*, is proposed as a suitable model for such studies, since different variants of exploded lekking have been described or proposed as the dominant mating system in many bustard species. The actual evidence on mating systems in this family is reviewed, especially regarding the better studied species, the Great Bustard *Otis tarda* and the Little Bustard *Tetrax tetrax*. Finally, the importance of mating systems for the conservation biology of those and other exploded lekking species is discussed.

Key words: bustards, conservation, exploded leks, female choice, lek evolution.

RESUMEN.—Leks *dispersos: lo que nos enseñan las avutardas.* En los sistemas de emparejamiento de tipo *lek*, los machos defienden pequeños territorios de exhibición agregados que las hembras visitan para copular (Höglund & Alatalo, 1995). Una especie formadora de *leks* ha de cumplir cuatro condiciones (Bradbury 1981): (1) no existe cuidado parental por parte del macho; (2) los machos se congregan en lugares concretos para llevar a cabo las paradas o exhibiciones sexuales; (3) el único recurso que las hembras encuentran en los *leks* está constituido por los genes de los machos; (4) las hembras pueden seleccionar a su pareja(s). Por otra parte, numerosos estudios han mostrado la existencia de sistemas de emparejamiento que no cumplen por completo estas condiciones, pero que todavía deben ser considerados *leks*. Los «*leks* dispersos» constituyen

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una de las principales categorías de tales *leks* «no clásicos» (Gilliard, 1969; Emlen & Oring, 1977). En los *leks* dispersos, los machos se exhiben separados por distancias considerables y su nivel de agregación no se detecta hasta que no son cartografiados sobre una superficie suficientemente amplia (Bradbury, 1981). Consecuentemente, los machos defienden territorios más extensos en los que las hembras pueden alimentarse e, incluso, anidar (Ligon, 1999), lo que incumple, en principio, la tercera condición propuesta por Bradbury. En este artículo se presenta una revisión de los principales aspectos relacionados con los sistemas de emparejamiento de tipo *lek* disperso en aves, incidiendo en la relevancia de los mismos en el estudio de la elección de pareja y de la evolución del *lek* como sistema de emparejamiento, dado su carácter intermedio entre los *leks* clásicos y la poliginia basada en la defensa de recursos. Se propone a la familia de las avutardas y sisones, *Otididae*, como modelo apropiado para dichos estudios, puesto que los *leks* dispersos han sido descritos o propuestos como sistemas de emparejamiento dominantes en muchas de sus especies. Se revisa, igualmente, la información disponible sobre los sistemas de emparejamiento en esa familia, especialmente la relativa a las especies mejor estudiadas, la Avutarda Común *Otis tarda* y el Sisón Común *Tetras tetrax*. Por último, se discute la importancia de los sistemas de emparejamiento para la biología de la conservación de éstas y otras especies formadoras de *leks* dispersos.

Palabras clave: conservación, elección de pareja, evolución de los *leks*, *leks* dispersos, otídidas.

INTRODUCTION

Lekking has been described in many avian families (see reviews in Oring, 1982; Johnsgard, 1994; Höglund & Alatalo, 1995; Jiguet *et al*., 2000), which are otherwise largely dominated by monogamous species. Lekking is a type of mating system in which males defend small, clustered courts (also called leks or lek arenas) that females visit in order to mate (Höglund & Alatalo, 1995). Bradbury (1981) suggested four criteria to identify a lekking species: (1) there is no male parental care, so that males contribute nothing to the next generation apart from gametes; (2) males aggregate at specific sites for display; (3) the only resource females find at the lek are the males themselves, that is, male genes; (4) females can select their mate(s), although the necessity of this latter condition has been highly debated, particularly in the case of vertebrates (see Höglund & Alatalo, 1995).

According to Bradbury's criteria, we can thus define classical leks as a non resource-based (or non-economic) mating system, in which females select mates among males that show complex morphological and behavioural traits specifically evolved to attract females (see review in Johnsgard, 1994), but whose direct contribution to the fitness of their offspring seems very small. Among birds, classical leks are found, for example, in several grouse (e.g. Black Grouse *Tetrao tetrix*, Sage Grouse *Centrocercus urophasianus*), scolopacids (e.g. Ruff *Philomachus pugnax*, Great Snipe *Gallinago media*), birds of paradise (e.g. Raggiana Bird of Paradise *Paradisea raggiana*), cotingids (e.g.

Cock of the Rock *Rupicola rupicola*) and manakins (see reviews in Oring, 1982; Johnsgard, 1994; Höglund & Alatalo, 1995; Jiguet *et al*., 2000). Nevertheless, many studies in other species have revealed the existence of mating systems that do not fit completely Bradbury's conditions for classical leks, but that still should be considered as leks. One of the main categories of non-classical leks is the so-called «exploded» or «dispersed» leks (Gilliard, 1969; Emlen & Oring, 1977; Snow, 1985; Höglund & Alatalo, 1995). In exploded leks, males within a display assemblage are separated by considerable distances. Aggregation might not even be detectable until males are carefully mapped over a large area (Bradbury, 1981). One consequence of the lower level of aggregation found in exploded leks is that males can hold large territories within which females can potentially forage and even nest (Ligon, 1999), therefore failing to fulfil criteria 3 from Bradbury's definition. In the extreme, species where male display sites include resources critical for females are said to be resource-based leks (Alexander, 1975).

Lek mating systems and lekking behaviour have become some of the most studied issues in behavioural and evolutionary ecology over the last three decades. Leks have received much attention for two main reasons (Ligon, 1999). First, they give rise to the question of why males congregate at a single site to mate, that is, what is the advantage, if any, of male clustering both for males and females. Secondly, they provide an *a priori* excellent scenario for the study of sexual selection. This second aspect of leks was already pointed out by Darwin (1871) and

has been highlighted in the last years by Trail (1990): 'The potential for sexual selection reaches full expression in species with lek mating systems'. Such potential originates from the fact that male clustering leads to an easier assessment of different males by females, and thus potentially to a high variance in male mating success if females concur in their choices among males (Andersson, 1994; Höglund & Alatalo, 1995; Ligon, 1999). In classical leks, females apparently show a strong discriminating capacity to select mates, sometimes reaching high levels of consensus (see, for example, Payne, 1984; Bradbury *et al*., 1985; Gibson & Bradbury, 1985). On the contrary, in resource-based mating systems, where the economic benefits for females in mating with a good male might be important (Thornhill, 1976; Gwyne, 1984; Alatalo *et al*., 1986), mate choice intensity seems less developed. This contradiction has been called the «lek paradox» (Borgia, 1979). Furthermore, this paradox has also another aspect: in leks, choosy females generally prefer males with the most exaggerated secondary traits, presumably because these traits indicate males carrying genes of the highest quality. However, if strong selection occurs, genetic variation should be exhausted in a few generations and, subsequently, females would gain nothing from their choice (Taylor & Williams, 1982 ; Kirkpatrick & Ryan, 1991). The lek paradox has attracted much theoretical attention, as we will discuss later. Finally, the mechanisms of lek formation and its evolution are still far from being fully understood.

The aim of this forum contribution is twofold: first, to highlight the theoretical importance of exploded leks for understanding the main issues of the study of lek mating systems; second, to emphasise the suitability of bustard species as models for the study of exploded leks, as grouse have been the most suitable models for the study of classical leks. Finally, we also discuss (through the example of bustards) the importance that such a theoretical issue might have on practical conservation issues.

EXISTING EVIDENCE ON LEK MATING SYSTEMS IN THE FAMILY *OTIDIDAE*

Exploded lek mating systems are found in different avian families and species (Johnsgard 1994; Höglund & Alatalo, 1995), including grouse, bustards and birds of paradise. One of the families in which exploded leks seems to be most widespread is the bustard family *Otididae*. Although the basic breeding biology of most bustard species remains largely unstudied, the existing evidence clearly points in that direction (see also Jiguet *et al*., 2000). The two better studied species, namely the Great Bustard *Otis tarda* and the Little Bustard *Tetrax tetrax,* have typical exploded lek mating systems, although each one has its own peculiarities (Schulz, 1985; Carranza *et al*., 1989; Hidalgo & Carranza, 1990; Morales *et al*., 1996; Morales, 1999; Jiguet *et al*., 2000; Jiguet, 2001). Recent studies on Houbara *Chlamydotis undulata* and Kori *Ardeotis kori* Bustards have also shown that exploded leks are also the most probable mating system in those species (Gaucher, 1995; Osborne & Osborne, 1998, 2000).

Available information on mating systems among bustards is compiled in Table 1, which highlights that exploded leks are the predominant mating system in the family. Monogamy has been cited for some species. However, those species are very poorly studied and categorisation of their mating system is based mainly on isolated observations of «paired» individuals and on the fact that they are monomorphic in size (Johnsgard, 1991; Del Hoyo *et al*., 1996), in spite of the fact that their basic breeding biology remains unknown. Although the latter affirmation also holds for some of the bustard species considered as «exploded lekkers» in Table 1, the fact remains that dispersed lekking is the main mating system among well-known bustards. Moreover, both size and plumage monomorphims are also found among other lekking birds (Höglund, 1989; Höglund & Alatalo, 1995).

The two species of *Otididae* in which the mating system has been best studied are the Great Bustard (Gewalt, 1959; Sterbetz, 1981; Carranza *et al*., 1989; Hidalgo & Carranza, 1990; Hellmich, 1991; Morales, 1999) and the Little Bustard (Schulz, 1985; Jiguet *et al*., 2000; Jiguet, 2001). In both cases, exploded lekking seems to be the main mating strategy. However, it is important to keep in mind that mating systems are flexible and can vary in the same species, and even in the same population, depending of different factors such as female dispersal, resource distribution and habitat sta-

TABLE 1

Existing evidence on mating systems in the family *Otididae*. Parentheses indicate that the type of mating system is only supposed.
[Tipos de sistema de emparejamiento descritos en la familia Otididae. *Exploded lek:* lek *disperso; isolated males: machos aislados; monogamy: monogamia. Los paréntesis indican que el tipo de sistema de apareamiento es supuesto, no comprobado.]*

Species	Mating System	Sources
Otis tarda	exploded lek	Gewalt, 1959; Morales, 1999
Ardeotis arabs	(exploded lek)	Del Hoyo *et al*., 1996
A. kori	exploded lek	Osborne & Osborne 1998, 2000
A. nigriceps	exploded lek	Ali & Rahmani, 1984
A. australis	exploded lek	Fitzherbert,1978
Chlamydotis undulata	isolated males-exploded lek	Collins, 1984; Del Hoyo *et al*., 1996
Neotis ludwigii	exploded lek	Del Hoyo *et al*., 1996
N. demhami	exploded lek	Tarboton, 1989
N. heuglinii	exploded lek	Del Hoyo *et al*., 1996
N. nuba	(exploded lek)	Del Hoyo *et al*., 1996
Eupodotis senegalensis	monogamy	Johnsgard, 1991
E. caerulescens	monogamy	Johnsgard, 1991
E. vigorsii	monogamy	Johnsgard, 1991
E. rueppellii	monogamy	Johnsgard, 1991
E. humilis	monogamy	Johnsgard, 1991
Lophotis savilei	(exploded lek)	Del Hoyo *et al*., 1996
L. gindiana	(exploded lek)	Del Hoyo *et al*., 1996
L. ruficrista	exploded lek	Urban *et al*., 1986
Afrotis afra	exploded lek	Urban *et al*., 1986
A. afraoides	(exploded lek)	Del Hoyo *et al*., 1996
Lissotis melanogaster	exploded lek	Schulz, 1986
L .hartlaubii	(exploded lek)	Del Hoyo *et al*., 1996
Houbaropsis bengalensis	exploded lek	Rahmani *et al.,* 1990
Sypheotides indica	exploded lek	Rahmani *et al*., 1990
Tetrax tetrax	exploded lek	Schulz, 1985; Jiguet *et al*., 2000

bility (Davies, 1991; Ligon, 1999). In the case of the Great Bustard, for example, several stages in a gradient that ranges from clumped classical leks to harem polygyny and even monogamy have been proposed (see Table 2 and review in Morales *et al*., 1996). Nevertheless, most studies point to classical and exploded leks, and long-term studies and the monitoring of individually-marked birds have in fact shown that exploded leks are the most likely mating system in this species (Morales, 1999; Alonso *et al*., 2000; Alonso *et al*., 2001). According to these authors, Great Bustard males undergo a significant variation in their aggregation level throughout the mating season. They begin to display in large, compact flocks (month of March in their study sites) and end up strutting solitarily, though normally within visual reach of each other, and dispersed over a large but clearly delimited area of the total

available habitat (Morales *et al.,* 1996; Morales, 1999). The mating peak is reached during the dispersal phase, which normally occurs in the second week of April (Morales, 1999). Another interesting feature of lekking in the Great Bustard is that males do not hold exclusive territories during the mating season, but rather largely overlapping home ranges without fixed display sites (Hidalgo & Carranza, 1990; Morales, 1999), thus forming a so-called mobile or detached lek (Johnsgard, 1994). On the other hand, Little Bustard males establish their dispersed territories at the beginning of the season. These territories are held and defended throughout the mating period (Schulz, 1985; Jiguet *et al*., 2000) although varying degrees of within-season territorial turnover and satellite behaviour have recently been described (Jiguet, 2001). However, display in compact and mobile flocks has also been observed occasionally in

Mating system assessment in the Great Bustard. Several stages have been proposed in a gradient that ranges from clumped classical leks to harem polygyny and even monogamy.
[Sistemas de emparejamiento atribuidos a la Avutarda Común. Se han propuesto diversos estados de un gradiente que varía entre lek *clásico y monogamia, pasando por la poliginia en harenes.]*

Mating system	Sources
Classical lek *[Lek clásico]*	Gewalt, 1959; Cramp & Simmons, 1980; Carranza *et al*., 1989
Exploded lek *[Lek disperso]*	Hidalgo & Carranza, 1990; Morales *et al*., 1996; Morales, 1999
Resource-based polygyny *[Poliginia basada en los recursos]*	Carranza *et al*., 1989; Hidalgo & Carranza, 1990
Harem-based polygyny *[Poliginia basada en harenes]*	Sterbetz, 1981; Carranza *et al*., 1989; Hidalgo & Carranza, 1990
Isolated promiscuity *[Promiscuidad con machos aislados]*	Sterbetz, 1981
Monogamy *[Monogamia]*	Sterbetz, 1981

the Little Bustard, very early in the breeding season (early April) and in populations with very high breeding density (ca. 17 males per km^2 in Crau, southern France; F. Jiguet, unpubl. data).

EXPLODED LEKS AND THE DEFINITION
OF LEKKING BEHAVIOUR

Broader definitions of leks than Bradbury's have been proposed in more recent years in order to include non-classical types. For example, Lewis (1985) defined leks as «a group of breeding males that regularly congregate on a fixed area (commonly referred to as an *arena*) to perform courtship display». Another broad definition of lek is the one provided by Höglund & Alatalo (1995): «male display aggregations that females attend primarily for the purpose of mating». In these broader definitions, the emphasis is put on the clustering of males on the display sites.

In classical lek species, males are highly aggregated and female home ranges are much larger than those of the males, which hold no resources. In resource-defence polygyny systems, the home range of both males and females is similar, as females feed and breed within the territories defended by males (Fig. 1). With regard to the level of male clustering and relative sizes of male and female home ranges (see Fig. 1), exploded leks occupy an intermediate posi-

tion in the gradient that goes from classical leks to resource-defence polygyny (Höglund & Alatalo, 1995; Ligon, 1999). The continuous variation in the gradient of male aggregation poses the problem of whether there are threshold levels to identify different lekking systems. This is well illustrated by two scolopacid birds, the Ruff and the Great Snipe. In the former, male territories are only a few square metres in size (van Rhijn, 1990), while in the latter they extend over some 100 square metres (Höglund & Robertson, 1990). Yet, both species are considered classical lekkers (Hogan-Warburg, 1966; Lemnell, 1978), since females do not make any use of male territories apart from visiting them to select a mate. On the contrary, in several exploded lekking species, females are known to feed and even nest within male territories. That is the case of both Great Bustard (Alonso *et al*., 2000) and Little Bustard (Jiguet *et al*., 2000) females, although female home ranges are still larger than male territories in these species (Fig. 1). Additionally, the level of male aggregation can vary in the same population between and within years, depending on variables such as population density, female encounter rate or habitat availability (Höglund & Alatalo, 1995). For example, within-season shifts from tighter to looser aggregations have been described in the Buff-breasted Sandpiper (*Tryngites subruficollis*; Pruett-Jones, 1988)
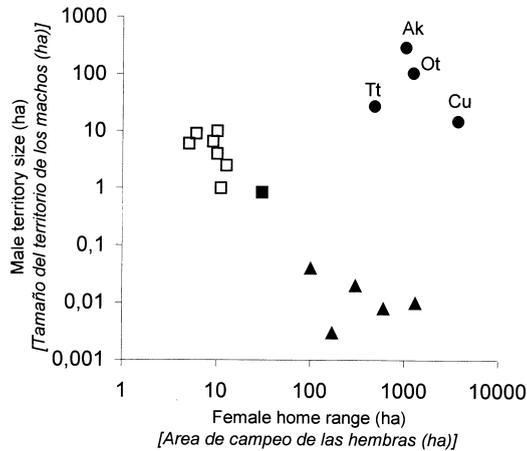
FIG. 1.—Male territory size in relation to female home-range size in grouse (subfamily Tetraoninae) and bustard species. Open squares: non-lekking grouse; closed square: exploded lekking grouse; closed triangles: lekking grouse; closed circles: exploded lekking bustards. Tt: *Tetrax tetrax*, Ot: *Otis tarda*, Cu: *Chlamydotis undulata*, Ak: *Ardeotis kori*. Sources: Höglund & Alatalo (1995) for grouses, Jiguet & Bretagnolle (pers. obs.) for the Little Bustard, Alonso & Morales (pers. obs.) for the Great Bustard, Urban *et al.* (1986) and Gélinaud *et al.* (1997) for the Houbara Bustard male and female home-ranges, respectively, and Osborne & Osborne (2000) for the Kori Bustard.

[Tamaño del territorio del macho en relación al tamaño del área de campeo de las hembras en distintas especies de las familias Tetraonidae y Otididae. Cuadrados blancos: tetraónidas sin lek; *cuadrado negro: tetraónidas con* lek *disperso; triángulos negros: tetraónidas con* lek *clásico; círculos negros: avutardas con* lek *disperso. Tt:* Tetrax tetrax, *Ot:* Otis tarda, *Cu:* Chlamydotis undulata, *Ak:* Ardeotis kori. *Fuentes bibliográficas: Höglund & Alatalo (1995) para las tetraónidas, Jiguet & Bretagnolle (obs. pers.) para el Sisón Común, Alonso & Morales (obs. pers.) para la Avutarda Común, Urban* et al. *(1986) and Gélinaud* et al. *(1997) para la Avutarda Hubara y Osborne & Osborne (2000) para la Avutarda Kori.]*

and the Great Bustard (Morales *et al.*, 1996; Morales, 1999). The latter reinforces the idea, as pointed out by Höglund & Alatalo (1995), that the difference between different lek systems is not clear-cut, but a continuum.

Consequently, the critical point to determine the mating system in non-classical leks is not the level of male aggregation, but whether resources play or not a determinant role in male distribution and female mate choice. Male clustering may be due to a patchy distribution of the resources required by females to ensure a successful breeding, or simply follow display site availability. In those cases, we shall not be dealing with true lekking behaviour, but with the so-called resource-based leks (Alexander, 1975) or with «landmark aggregations» (Höglund & Alatalo, 1995). Although resource-based leks are mainly found in insects (Thornhill & Alcock, 1983), they are well exemplified among birds by some hummingbird species, in which displaying males cluster around patches of flowers on which a particular species has specialised (Stiles & Wolf, 1979). Aggregations on landmarks are also mainly confined to insects (see Thornhill & Alcock, 1983; Alcock & Smith, 1987), but they have also been described in the McGregor's Bowerbird (*Amblyornis macgregoriae*; Pruett-Jones & Pruett-Jones, 1982), formerly thought to form exploded leks (Gilliard, 1969).

However, in either situation of classical, exploded or resource-based leks, males would benefit from setting up territories next to resources because this is where females are likely to be encountered (Bradbury, 1981). Therefore, it is not the absence of resources within territories that should distinguish lekking from non-lek-

king species, but the degree to which males regulate female access to those resources in order to obtain matings (Bradbury, 1985) or, in other words, whether female mate choice is influenced not only by the male characteristics but also the resources that he defends. In summary, a mating system cannot be considered as a lek if male territorial resources explain a part of the variance in male mating success. In this context, if the level of male aggregation and the influence of resources in male distribution have not been correctly assessed, an apparent exploded lek situation may actually turn out to be a resource-based polygyny, promiscuity or a solitary display mating system (see discussion on this respect by Carranza, 1992).

As Jiguet *et al*. (2000) have pointed out, bustard species seem, indeed, to be good models for the assessment of the relationship between resources, individual quality, and female mate choice. Specifically, these authors tested how the Little Bustard in western France fits the criteria of male aggregation and of lack of resources in male territories involved in female choice. They not only determined the degree of male clustering, but also tested the independence of male spatial distribution with respect to that of suitable display habitat, which discarded the possibility of landmark aggregations. In relation to resources in male territories, they found that these were mainly selected according to male requirements (food and good display conditions) rather than to females' (food, but also shelter for nests provided by permanent crops). Furthermore, females did not apparently use the amount of resources defended as a criterion for mate choice, as male attractiveness was not related to the resources within their territories. Consequently, lekking behaviour is truly present in the species. They argued, however, that where habitat suitability is strongly decreasing due to agricultural intensification, exploded leks can easily change into resource-based leks as a result of concentration of displaying males in the remains of suitable habitat. That seemed to be the case for their study population. They further argued that, in a rapidly declining population like those they studied in western France, resource-based leks could also change into resource-based polygyny following a further decline in bird density. This type of approach is still lacking in the study of Great Bustard leks, but it would be very enlightening given the range of mating strategies mentioned in the literature for this species.

EXPLODED LEKS AND FEMALE MATE CHOICE

As previously stated, lekking behaviour is associated to what was defined as the lek paradox (Borgia, 1979) in relation to the intensity in female mate choice and the choice for «good genes». If females choose males with the most exaggerated secondary traits as a cue for the genes of highest quality, unanimous female choice for these males would lead to a rapid loss of variation in male genetic quality and, subsequently, females would gain nothing from their choice (Taylor & Willimas, 1982; Kirkpatrick & Ryan, 1991).

Pomiankowski & Møller (1995) proposed a solution for the lek paradox. These authors showed that genetic variability of secondary sexual traits is higher than that of non-sexual ones. Higher genetic variability among sexual traits can be explained if they are subject to directional selection that is stronger than linear because this selects for greater phenotypic variation. That would explain the absence of fixation of advantageous male traits despite the extreme consensus of female choice found in leks. Their conclusion is, therefore, that there exists no lek paradox.

More generally, at the true heart of the paradox, there is the question of why should females in leks have evolved such strong mate selection when they seem to receive no tangible benefit from their choice (Kirkpatrick & Ryan, 1991). This question is not addressed by Pomiankowski and Møller's (1995) assessment. The lek paradox can be expressed in terms of the direct costs and benefits for females of mate search (Reynolds & Gross, 1990), as graphically represented in Figure 2. The direct costs of searching for a mate increase arithmetically with search effort (e.g. time devoted to search), while the potential benefits will follow a diminishing rate curve. In resource-based mating systems, benefits are higher and, therefore, for an equal rate of increase of costs, the maximal difference between benefits and costs, that is, the net benefits of mate search, are higher. The intensity of mate search at which the optimal net benefits are reached can provide an idea of

the level of female «choosiness». In a lek paradox scenario (Fig. 2a), such level is greater in economic systems, which is in contradiction with observation of animal mating systems. Table 3 shows some of the direct (in relation to female fitness) costs and benefits of female mate choice proposed in the literature.

Reynolds & Gross (1990) suggested three possible solutions to the lek paradox: (1) benefits of mate search are higher in leks than in resource-based mating systems, (2) costs are lower in leks than in economic mating systems, and (3) both costs and benefits are lower in leks than in resource-based mating systems. For these authors, the third solution is the most plausible one (see Fig. 2b) since it predicts that, even if benefits are lower, in non-economic mating systems females may search for mates among more males, or for longer periods of time, because costs of search are low.

The intermediate stage occupied by exploded lekking in the continuum between resource-based polygyny and classical leks makes them a good scenario to study how costs and benefits of female mate search can vary along such gra-

dient. It places female «choosiness» at a balance between the costs and benefits of mate choice in non economic mating systems and those in economic ones, as shown in Figure 2c. The potential for female choice would consequently be higher in exploded leks than in classical ones, since the possibility of exploiting the resources present in male territories during visits, along with a reduced level of male-male interference, would allow females to stay longer and to make a better assessment of male phenotypic quality according to their own preferences, thus increasing the benefits of mate search. Therefore, exploded lekking species seem to be appropriate models for the study of mate choice.

Figure 2c also shows that the point at which costs of mate search overrun benefits ($C_{EL} > B_{EL}$) would be reached earlier in exploded leks than in classical ones. This would mean that any habitat perturbation that increased the costs of mate search in any given population would favour the development of resource-based polygyny systems rather than classical leks and, therefore, that the above mentioned balance is

TABLE 3

Some examples of the potential direct costs and benefits of female mate choice in lek mating systems. Based on Reynolds & Gross (1990) and Johnsgard (1994).
[Algunos de los costes directos y beneficios potenciales para la hembra de la elección de pareja en los sistemas de emparejamiento de tipo lek. *Basado en Reynolds & Gross (1990) y Johnsgard (1994).]*

| Potential costs	Potential benefits
Difficulties in assessing the fittest males *[Dificultad para evaluar cuáles son los machos más aptos]*	Access to many males to choose from *[Acceso a numerosos machos entre los cuales elegir]*
Increased predation risk *[Aumento del riesgo de depredación]*	Greater fertilisation probabilities *[Mayores probabilidades de fertilización]*
Travel time and energy expenditure *[Gasto de tiempo y energía durante los desplazamientos]*	Safety from copulation disruption in hierarchical leks *[Evitación de las interrupciones de cópulas en los* leks *jerárquicos]*
Competition with other females *[Competencia con otras hembras]*	Avoidance of diseases and parasites *[Evitación de infecciones y parásitos]*
Risk of injury by other individuals in non hierarchical leks *[Riesgo de lesiones por parte de otros individuos en* leks *no jerárquicos]*	
Risk of copulation disruption by other males *[Riesgo de interrupción de cópulas por otros machos]*	
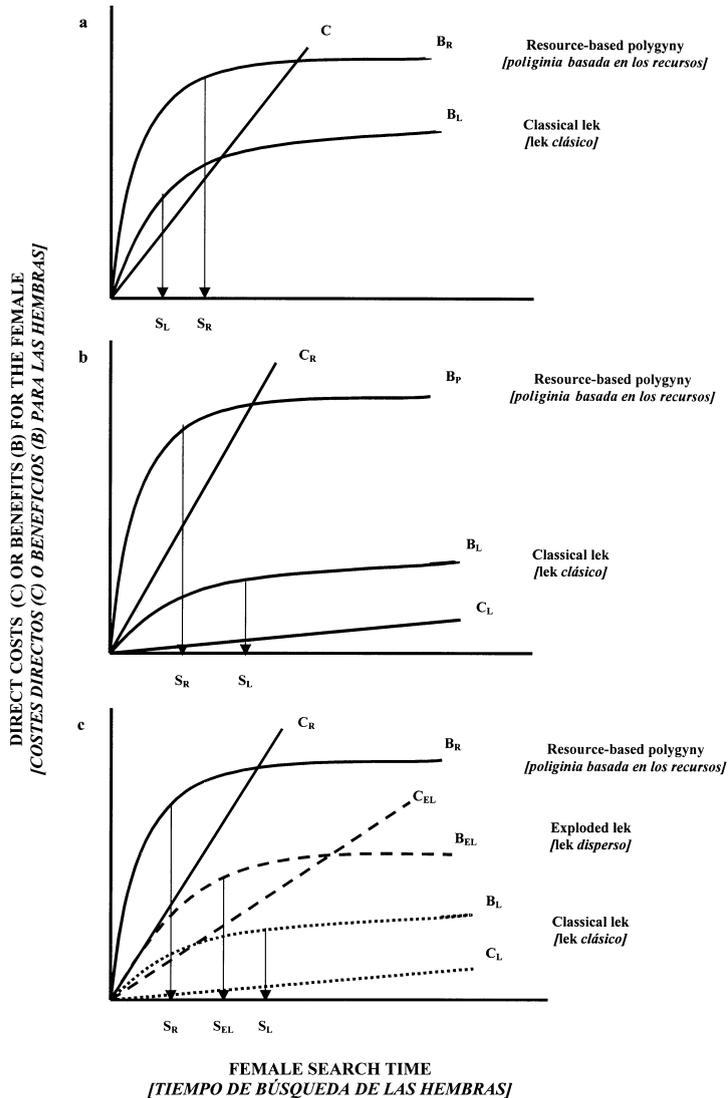
FIG. 2.—Cost and benefit curves of mate search by females. a) Lek paradox scenario where benefits of search in a resource-based mating system are higher than in a lek mating system, while costs remain equal. b) A possible solution of the lek paradox, in which both benefits and costs of mate search are lower in lekking than in resource-based mating systems. c) Intermediate position of exploded leks in relation to classical leks and resource-based mating systems. Arrows indicate the point of maximum net benefits in each situation. Based on Reynolds & Gross (1990).

[Curvas de costes y beneficios de la búsqueda de pareja por parte de las hembras. a) Situación de «paradoja del lek», *en la que los beneficios de la búsqueda en un sistema de emparejamiento basado en la defensa de recursos son mayores que en un sistema de tipo* lek, *mientras que los costes permanecen iguales. b) Una posible solución de la paradoja del* lek, *en la cual tanto costes como beneficios de la búsqueda de pareja son inferiores en los sistemas de emparejamiento de tipo* lek *que en los basados en la defensa de recursos. c) Situación intermedia de los* leks *dispersos en relación a los leks clásicos y a los sistemas de emparejamiento basados en la defensa de recursos. Las flechas indican el punto de máximo beneficio neto en cada situación. Basado en Reynolds & Gross (1990).]*

not bidirectional but mainly unidirectional. Such prediction could be tested in populations in which suitable male display sites have become more dispersed over time due to, for example, agricultural intensification in the case of both Great and Little Bustards.

Finally, when trying to identify criteria for mate choice by females, one should measure or evaluate male mating success. Ideally, this should be attained by directly assessing the proportion of offspring sired by each male through DNA fingerprinting of hatchlings. Given the practical difficulties of such approach, mating success in lekking species is generally measured through copulation rate. Copulations are easily observed in classical lek species, where males display and females mate on the arena. However, this is not normally feasible when studying exploded lek species. Males are relatively dispersed and thus cannot be monitored simultaneously, so that it is not possible to obtain extensive data on copulation events. The only practical way to evaluate male mating success on exploded leks is to obtain an indirect measure of copulation success, usually the attractiveness of males to females. This is legitimate because in studies of classical lekking birds where both have been assessed, this measure is highly correlated with number of copulations (Andersson, 1992; Rintamäki *et al.*, 1995a). Moreover, male attractiveness has also been considered in some classical lekking species (Höglund & Robertson, 1990; Fiske & Kålås, 1995; Rintamäki *et al.*, 1995a, 1995b; Gibson, 1996).

The mentioned difficulties to measure copulation success in exploded leks are well illustrated both by Great and Little Bustards. In the former, during a three year study of 17 radio-tagged males in Villafáfila, north-western Spain, only five copulations were recorded, two of them performed by the same individual (Morales, 1999). Copulations by non-tagged individuals were, however, more frequently seen, which allowed the study of copulation timing. Nevertheless, numbers always remained very low (*n* = 16 for the three years of study; Morales, 1999) in comparison to those obtained in classical lekking species, and especially so if we consider that the study was carried out in the world's densest population of the species (see Alonso *et al.*, 1996). The scarcity of copulation records is even more important for the

Little Bustard, where only one copulation was observed during a 4-year study in western France (Jiguet, 2001). In both cases, male attractiveness, defined as the number of copulation attempts (successful or not) per male in the Great Bustard study (Morales, 1999), as well as the frequency with which a given male was detected alone in the company of one or more females in studies of both species (Morales, 1999; Jiguet, 2001), was used as an indirect measure of male mating success.

EXPLODED LEKS AND THE EVOLUTION
OF LEK MATING SYSTEMS

There are four basic theories to explain the occurrence of male clustering on leks (see reviews in Höglund & Alatalo, 1995; Ligon, 1999). The hotspot model (Bradbury & Gibson, 1983; Bradbury *et al.*, 1986) suggests that males cluster in areas where the female density is highest. A second model is the female preference model (Bradbury, 1981; Bradbury & Gibson, 1983; Beehler & Foster, 1988), which states that females prefer to mate with males in larger leks for varying reasons such as reduced costs of search and assessment of potential mates. Thirdly, the hotshot model proposes that females prefer to mate with a particular type of males, and that suboptimal males aggregate around attractive ones to parasite their attractiveness (Arak, 1982; Beehler & Foster, 1988). The hotshots are therefore attractive to females but also to males. Finally, the black hole model highlights the role of sexual harassment by males (Clutton-Brock *et al.*, 1992). Females have no preference for any particular male, as long as they are not harmed due to harassment by males during courtship and mating. They tend to avoid the more harassing males and leave their territories. However, since they eventually must mate, they benefit by doing so with the male in whose territory they happen to be present, thus minimizing their time of stay at the lek and reducing the risk of injury. Leks arise because the probability that males retain females are much higher if they are clustered than if they are solitary (Stillman *et al.*, 1993).

Studies on exploded lek species can shed light on the evolution of lek mating systems. It has been suggested that exploded leks evolved

from classical leks due to a compromise between the females' interest in having males clustered and the interest of males for avoiding disruptions in highly clumped leks (Foster, 1983). In contrast, other authors consider more plausible an evolutionary scenario in which exploded leks are precursors of classical leks (Théry, 1992; Ligon, 1999). Exploded leks thus seem to offer a good scenario for the study of mechanisms of lek formation (see reviews in Höglund & Alatalo, 1995; Ligon, 1999). This is especially true for those mechanisms independent of male-male interactions, like the female preference and hotspot models which suggest mechanisms driven by female choice, since reduced male interference due to greater distances between male territories allows direct or experimental evaluation of female choice. The use of artificial leks for testing models involving female preferences holds great potentialities in exploded lek species.

CONSERVATION IMPLICATIONS OF LEKKING BEHAVIOUR

Knowledge of the basic biology and ecology of a species has proved to be critical to establish efficient conservation and management strategies (see, for example, Caro, 1997). Studying a species' mating system and assessing mechanisms of male and female distributions, as well as the processes determining female choices and the role of resources, provides evident conservation cues. Given that most bustard species are actually in decline (Del Hoyo et al., 1996), a research effort should be made in order to understand and correct the causes of such a tendency. For example, the study on Little Bustard mating systems and strategies has proved very important in order to determine effective conservation measures for the species (Jiguet et al., 1998). Indeed, it has highlighted that male and female needs are not necessarily similar, and thus that conservation measures directed to increase reproduction might be different than those associated to male presence. Finally, the fact that females seem to be less attracted by small leks has also indicated how the decline may be faster than expected from population dynamic assessments, as some areas will be deserted when male density falls below a treshold value.

The importance of mating systems in conservation is also well exemplified in the case of the Great Bustard. One of the main conservation-relevant conclusions that can be drawn from the study of lekking dynamics in that species is that both males and females show a strong inter-annual fidelity to lekking and nesting sites (Alonso et al.,2000; Morales et al., 2000). As a result of that fidelity to traditional sites and of strong conspecific attraction, individuals do not tend to colonise vacant patches of suitable habitat but to concentrate in already occupied ones. Moreover, when a lek disappears as a consequence of habitat change or human interference, dispersing Great Bustards do not form new leks in vacant suitable habitat, but join the closest and largest already existing leks (Alonso et al., 2001), as predicted by theoretical models of conspecific attraction (Reed & Dobson, 1993; Danchin & Wagner, 1997). The result is an increased concentration of populations and, consequently, a greater vulnerability of the species to local catastrophes, as well as a greater risk of loss of genetic diversity, that may lead to extinction of smaller and more peripheral leks (Alonso et al., 2001). This tendency to concentration shows that a highly dense and even growing population (Alonso et al., 1996; Morales, 1999) does not necessarily imply a healthy status of the species at the metapopulation level. Moreover, the species' social system might be acting as an accelerating factor of the process. Yet, the knowledge of the social system should help in establishing an appropriate conservation policy, in this case maintenance and improvement of habitat in already existing nuclei to avoid further concentration and eventual density-dependent effects. Efforts to improve habitats that have been unoccupied for a long time pursuing their recolonization might be in vane, as highlighted by large portions of perfectly suitable habitat remaining largely unused (Lane et al., 2001).

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