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## Male sexual display and attractiveness in the great bustard *Otis tarda*: the role of body condition

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**Abstract** Individual display rates and attractiveness of 17 radio-tagged, free-living great bustard males in north-western Spain were studied in relation to the degree of development of secondary sex traits, body condition, and age. Variance in display rate was significantly explained by body condition and length of moustache feathers, and neck development and display rate significantly accounted for the variance in male attractiveness. Age did not present any clear association with display rate or attractiveness, and it was significantly correlated only with neck development. These results suggest a total viability scenario of female mate choice in which the advertisement of global fitness is based on condition-dependent phenotypic and behavioural traits.

**Key words** Attractiveness · Body condition · Display rate · Great bustard · Secondary sex traits · Total viability

### Introduction

Sexual selection in polygynous species, in which males compete to mate with the largest possible number of females and do not take part in parental care, is fundamentally expressed in two directly observable processes: the evolution of sexual dimorphism in size and/or morphology, and a certain bias in the distribution of male mating success (Darwin 1871; Payne 1984; Andersson 1994).

Male sexual dimorphism in size has been attributed, ever since Darwin (1871) first discussed it, to direct competition among males to monopolize females in an agonistic context, resulting in the establishment of dominance hierarchies. Similarly, intra-sexual selection has led, in many species, to the evolution of organs that function as “arms” in such agonistic interactions. On the other hand, the development of male morphological traits without apparent benefits to individual survival has been linked to female choice of those males showing a greater degree of development of such traits. Most studies thereafter agree in concluding that female mate choice is the factor responsible for the maintenance of secondary sex traits in males (e.g. Maynard-Smith 1991; Andersson 1994).

Evolutionary mechanisms involved in female mate choice in polygynous species can be classified into two main categories (Reynolds and Gross 1990; Kirkpatrick and Ryan 1991; Maynard-Smith 1991; Andersson 1994): those mechanisms directly activated by natural selection and thus providing offspring with a direct fitness benefit (e.g. resources important to female or offspring survival, reduced time and cost in mate search, avoidance of diseases and parasites), and those mechanisms producing genetic benefits (“good genes”) to descendants through the selection of either those males presenting certain traits not directly related to survival but linked to genes that increase offspring viability (pleiotropic effect), or those in a better physical condition as a phenotypic expression of their global fitness (total viability hypothesis, Manning 1985). An additional indirect mechanism is that associated with age as an indicator of male viability (Manning 1985; Andersson 1994). Females thereby should select those males showing a greater degree of development in ornaments and other traits positively related to age, given that older males must present a higher global fitness, since they have lived longer, thus presumably carrying a lower proportion of deleterious genes.

The great bustard *Otis tarda* is a ground-dwelling, lekking bird that inhabits natural and cultivated grasslands. Its status is endangered in most of its range, except in the Iberian Peninsula, which represents the main stronghold of

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the species (Alonso and Alonso 1996). It is one of the most sexually size-dimorphic bird species (Payne 1984), and males and females generally occur in separate flocks (Cramp and Simmons 1980; Hidalgo and Carranza 1990; Alonso et al. 1995). Between late winter and early spring males concentrate at traditional arenas where they fight to establish rank and then display in an exploded lek mating system (Hidalgo and Carranza 1991; Morales 1999; see Gilliard 1969 and Höglund and Alatalo 1995 for the exploded lek concept).

In this article, the display behaviour and attractiveness of a sample of radio-tagged great bustard males are studied in relation to the degree of development of secondary sex traits, body condition, and age for the period from immediately after the phase of hierarchy establishment, that is, just before the explosion of the lek, until the end of the main mating period (from late March to mid-May, Hidalgo and Carranza 1990; Morales 1999). Although these three aspects have been partly treated in a previous study on captive individuals (Carranza and Hidalgo 1993), it is the first time that results on display behaviour and individual differences in potential mating success of free-living great bustards are presented and discussed.

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## Study area

Our study was carried out in the Wildlife Reserve of Villafáfila (41°50'N, 5°35'W, about 700 m asl), which extends over 32,682 ha of dry, treeless, and gently undulating farmland in the Province of Zamora, north-west Spain. The land is almost entirely cultivated with wheat, barley, and a small proportion of alfalfa. The remaining surface (about 9%) is occupied by natural grassland used for sheep grazing. The Reserve holds the world's densest population of great bustards, with more than 2,000 birds at mating time in spring, and 650–750 breeding adult females in summer (Alonso et al. 1996).

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## Materials and methods

### Sample size

Great bustard males used in this study are classified into two sub-samples: (1) birds of known exact age, but unknown adult measurements ( $n = 10$ ): captured as chicks (1–2 months old) and marked with patagial tags between 1983 and 1993. These are birds that survived juvenile mortality and finally settled in the study area, so they could be further studied during adult life (from age 3 years onwards, see, for example, Glutz et al. 1973; Cramp and Simmons 1980); (2) birds of known adult measurements, but unknown exact age ( $n = 8$ ): captured as adults in the study area in 1993 and 1994 using rocket nets and provided with backpack transmitters and dorsal PVC tags for visual identification. These birds were weighed and measured during handling. For one of the

birds from sub-sample 2 it was possible to determine its exact age because it was easily identified as a 2-year-old male following Gewalt (1959). Therefore, the total sample of males studied is 17.

Marked males were tracked during 2–3 complete days per week over the mating seasons of 1995, 1996, and 1997 (from the last week of March to the 2nd week of May), concentrating observation effort during the morning (from dawn to 1300 hours) and evening activity peaks (from 1700 hours to dusk), since activity in general, and particularly sexual activity, was considered negligible around mid-day (see also Hidalgo and Carranza 1990; Martínez 2000). Observations were made from ground vehicles using 20–40×, 20–60×, and 60–90× telescopes. The number of observers varied between three and four; each observer tracked one male per day, so that the maximum period for each male without observations was 3 days, thus distributing observation effort uniformly among marked individuals.

### Data collection

Data collection consisted of ad libitum recording (Martin and Bateson 1993) of all significant behaviours and their duration. Each time an individual began to display, the duration of the display period was measured. The number of display events was recorded (see Gewalt 1959 for a full description of display behaviour in the great bustard). Simultaneously, changes in flock size and composition were also recorded ad libitum, as well as any variation in its location and that of surrounding flocks within a radius of 1 km from the marked male.

The time devoted to display by each male per period of observation was calculated. This value was divided by the total net time of observation during the corresponding 1-h period to obtain an hourly display rate. A mean value of hourly display rate, hereafter simply display rate, was calculated for each of the 17 males.

### Male categories

All males were categorised in relation to the degree of development of their neck. This classification was made on the basis of a visual assignment, both from direct observation and from photographs. Three categories of neck development were established (see Fig. 1). Category 1 was assigned to birds with completely grey necks spotted with brown at the base. This type of neck is characteristic of 1-year-old males and is scarcely different from that of adult females (see Gewalt 1959). Our sample did not include any males belonging to this category. Category 2 corresponded to necks clearly presenting a dark brown band at the base, above which there is a broad creamy yellow band that adjoins the grey colour under the lower mandible. Finally, category 3 was assigned to males with an intensely dark brown, mahogany-like band, narrower than that of category 2, followed upwards by a long ivory-coloured band reaching the bird's chin without transition to grey. Between these two

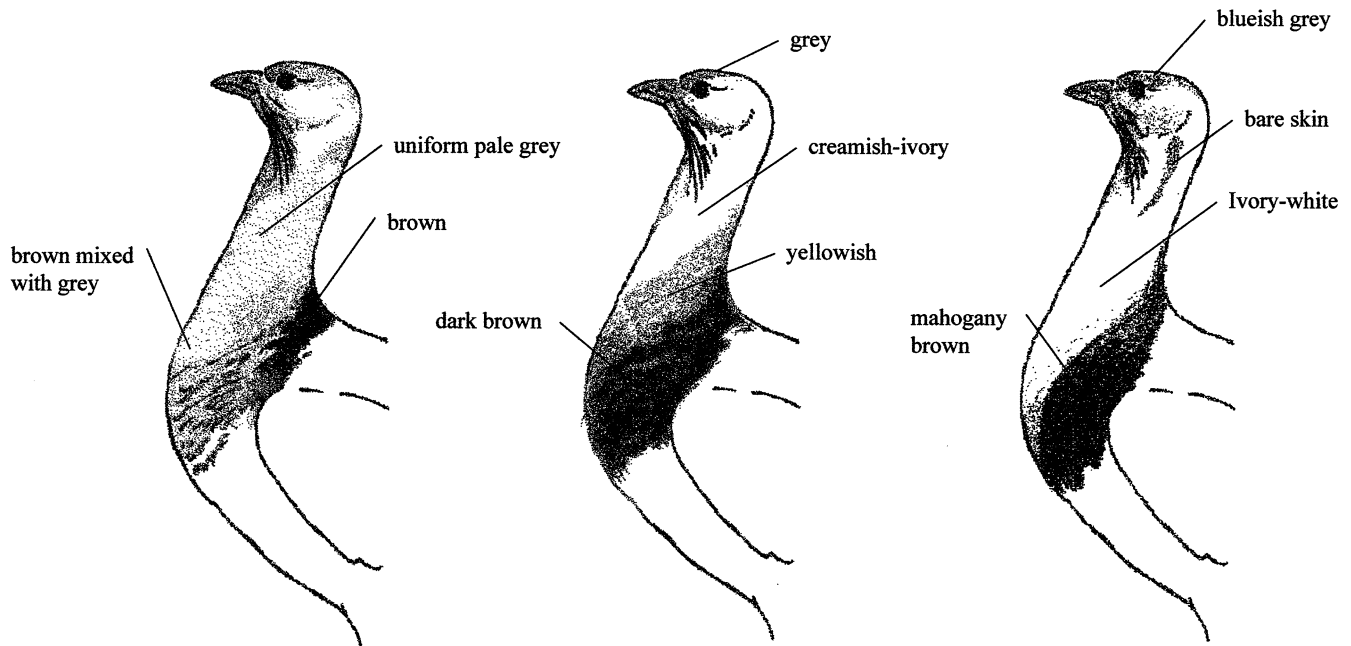


Fig. 1. Categorisation of male great bustard necks. *Left* Neck 1; *centre* neck 2; *right* neck 3. Intermediate types were given values 1.5 and 2.5

bands there is usually a narrow, more yellowish, transition band. Intermediate situations were given values of 1.5 and 2.5. Each male was categorised independently by four different observers, reaching a 95% agreement calculated through Kendall's concordance coefficient ( $W$ ; see, for example, Siegel and Castellan 1988).

#### Mating success

Ideally, individual male mating success should be measured or evaluated by directly assessing the proportion of offspring sired by each male through DNA fingerprinting of hatchlings. Given the practical difficulties of such an approach, mating success in lekking species is generally measured through copulation rate (see Höglund and Alatalo 1995). Copulations are easily observed on classical lek species, where males display and females mate on the arena. However, this is not normally feasible when studying exploded lek species (Jiguet 2001; Morales et al. 2001). 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 given that 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 and Robertson 1990; Fiske and Kålås 1995; Rintamäki et al. 1995a, b; Gibson 1996).

The number of effective copulations performed by marked males observed in the present study was very small

and clearly not sufficient to be statistically analysed ( $n = 5$ , two of them performed by the same male). Therefore, male attractiveness to females was used as an indirect measure of mating success of marked individuals. Male attractiveness was estimated as the number of observations per season in which a given male was detected in the company of females, that is, forming with them a single group, divided by that individual's total time of observation. This variable was called "accompanying frequency". This approach has been used in other bustard species forming exploded leks, such as the little bustard *Tetrax tetrax* (Jiguet 2001). Additionally, we used a second estimate of male mating success, considering the total number of copulation attempts and dividing it by that individual's total time of observation ("copulation attempt rate"). We defined copulation attempt as any occasion in which a female approached a marked male and ended up pecking the male's cloaca (see, for example, Hellmich 1991 for a full description of the great bustard copulation behaviour), irrespective of whether the courtship was interrupted afterwards or copulation was finally accomplished.

#### Data analysis

A first analysis was performed using Spearman rank correlation (Siegel and Castellan 1988) to determine which variables were significantly associated with display rate and the two estimates of male attractiveness. The following biometric and phenotypic variables were tested: moustache length, mean neck classification value, and weight divided by tarsus length, as a measure of male body condition (Brown 1996), as well as mean age over the study period. A further analysis using multiple step-wise regression (Sokal and Rohlf 1969) was carried out, considering only those variables previously

**Table 1.** Spearman correlation matrix of the variables analysed. *Above diagonal:* significance level and sample size. *Below diagonal:* Spearman correlation coefficients. *Question marks* indicate variables that could not be measured on adult great bustard males of known age

	Display rate	Accompanying frequency	Copulation attempt rate	Age	Weight/tarsus length	Moustache length	Neck development
Display rate	–	** (17)	* (17)	NS (10)	* (8)	* (8)	* (8)
Accompanying frequency	0.81	–	* (17)	NS (10)	* (8)	NS (8)	* (17)
Copulation attempt rate	0.57	0.61	–	NS (10)	* (8)	NS (8)	* (17)
Age	0.85	0.23	0.59	–	?	?	* (10)
Weight/tarsus length	0.78	0.7	0.79	?	–	NS (8)	NS (8)
Moustache length	0.84	0.44	0.48	?	0.58	–	NS (8)
Neck development	0.68	0.7	0.69	0.69	0.6	0.52	–

**Table 2.** Regression models accounting for variation in display rate and attractiveness of male great bustards

Dependent variable	Independent variable	Partial correlation coefficients	<i>F</i>	<i>df</i>	<i>R</i> <sup>2</sup>	<i>P</i>
Display rate	Weight/tarsus length	0.88	43.13	2, 5	0.95	0.0007
	Moustache length	0.89				
Accompanying frequency	Neck development	0.32	12.97	2, 14	0.65	0.0007
	Display rate	0.59				
Copulation attempt rate	Neck development	0.38	5.1	2, 14	0.42	0.02
	Display rate	0.26				

found to be significantly correlated with display rate and mating success. More specifically, three models were built. The first model accounted for individual variation in display rate and included the weight/tarsus index, moustache length, and neck development. Since no significant correlation between independent variables was found (see Table 1), multicollinearity can be considered negligible. All three independent variables were log-transformed, whereas display rate was normalized through arcsine transformation. The other two models accounted for the estimates of mating success and included only display rate and neck development as independent variables. To avoid multicollinearity no other correlate of display rate (e.g. weight/tarsus index) was considered. Both accompanying frequency and copulation attempt rate were normalized by means of log transformation. All statistical analyses were performed in STATISTICA 5.1 (Statsoft Inc. 1998).

## Results

Intensity of sexual display showed a significant dependence on body condition and secondary sex traits since display rate correlated with the weight/tarsus length index, moustache length, and neck development (Table 1). Furthermore, body condition and moustache length accounted for a very high percentage of the inter-individual variance in display rate as shown by the corresponding step-wise regression model (Table 2). Contrarily, age did not seem to be determinant in males' capacity of display, attractiveness to females, or mating success: mean age turned out to be significantly correlated only with neck development (Table 1).

Male attractiveness and mating success seemed to associate both with body condition and the development of sec-

ondary sexual traits, as well as with the intensity of sexual display. Accompanying frequency and copulation attempt rate were both significantly correlated with the weight/tarsus index and neck development, but not with moustache length. However, accompanying frequency showed a highly significant association with display rate, whereas copulation attempt rate was only marginally associated with this variable (Table 1).

The regression model for accompanying frequency accepted display rate and neck development. This model was very significant, showing that these independent variables can account for a high percentage of the variance in attractiveness to females among great bustard males (65% in the present study, Table 2). Finally, mating success seemed also to depend on neck development and display rate, although those variables explained a smaller proportion of the inter-individual variation in male copulation attempt rate (42%, Table 2).

## Discussion

The results presented show a high dependence of individual male display rate on phenotypic traits such as body condition and moustache length. The latter is a secondary sexual trait, exclusive to males and, therefore, directly involved in sexual selection. On the other hand, body condition largely determines to what extent an individual can afford the energetic costs of reproduction (see review in Clutton-Brock 1988 and Andersson 1994). Male attractiveness also seemed to be influenced by phenotype and more precisely, by neck development, and through its association with display rate, body condition, although this was not the case for the length of the moustache feathers. Display rate seemed to play a

significant role in explaining the variance of accompanying frequency, that is, the frequency with which a marked male was recorded in the exclusive company of females, although this association was weak when the frequency of copulation attempts was considered. Age was not associated with any of the dependent variables studied, although it was significantly correlated with neck development.

Several theoretical and empirical studies have suggested that the degree of development of most male secondary sexual traits depends on an individual's body condition (e.g. Williams 1966; West-Eberhard 1979; Kodric-Brown and Brown 1984; Andersson 1986; Folstad and Karter 1992). Such development can therefore be regarded as part of the reproductive effort made by males, which becomes greater as the physiological condition of the individual is better. Consequently, some phenotypic plasticity in the development of secondary sexual traits can be expected as a result of differences in each male's energetic budget (Andersson 1994). The results of the present study support the existence of such plasticity among great bustard males and the role of body condition in determining the intensity of sexual display in this species.

Sexual display has proved to be energetically costly in several polygynous and lekking bird species such as wild turkey *Meleagris gallopavo* (Badyaev et al. 1998) and sage grouse *Centrocercus urophasianus* (Vehrencamp et al. 1989). Given the elaborate and "ostentatious" display of great bustard males (see Gewalt 1959; Cramp and Simmons 1980; and Hellmich 1991 for descriptions), there are no reasons to believe that sexual exhibition in the great bustard is less costly than in other bird species with similar mating systems, as pointed out by Carranza and Hidalgo (1993). Both the significant decrease in time devoted to feeding found among males during the peak of sexual activity (Morales 1999) and the fact that many males are unable to fly at the end of the mating season, apparently as a consequence of exhaustion (personal observation), strongly suggest that the total energetic cost of sexual activity in great bustard males is considerable. The existence of an energetically costly display will thus produce inter-individual differences in display rate resulting from the varying body conditions of birds, as found in the present study.

The other variable explaining the inter-individual variance observed in display rate is moustache length, suggesting that this trait may function as an indicator of a male's capability to perform highly costly sexual displays. Although neck development was rejected from the regression model, it was significantly correlated with display rate, which suggests an association between neck pattern and intensity of display.

However, the association of neck development with male attractiveness reveals a potential role of this trait in female choice and, therefore, in male mating success. Neck development and display rate explain most of the variance of the first estimator of accompanying frequency. As discussed above, a good body condition is necessary to maintain high levels of display, during which neck patterns are conspicuously shown. Display intensity and neck pattern combined could therefore act as female attracting factors that produce

the grouping of females around displaying males. These two factors would continue functioning as cues for mate choice, as suggested by the regression model accounting for male attractiveness measured as the frequency of copulation attempts. The relatively low percentage of the total variance explained by the model probably indicates that other factors are operating in the process of mate choice (e.g. male rank hierarchy, female experience or courtship interruption by other conspecifics, as described for several lekking species; see review in Höglund and Alatalo 1995).

In relation to age, because birds of known age could not be measured as breeding adults, this variable could not be compared with body condition and moustache length. Consequently the role of age in moustache growth and the acquisition of good body condition and size could not be established. Carranza and Hidalgo (1993), however, found a significant correlation between age and moustache length, but they could not find any significant correlation between age and the number of moustache feathers or neck development. They concluded that moustache length was associated with ageing but not with body condition, and that differences in neck development were indicative of high variance in the physiological state of adult males, regardless of their age. The results presented here are partly contradictory to those obtained by Carranza and Hidalgo (1993). On one hand, neck development was correlated with mean age over the period of study, which suggests an age dependence of this secondary sexual trait involved in female attraction. On the other hand, the lack of correlation between age and display rate and male attractiveness leads to the conclusion that, regardless of age, the variance among adult males in their capacity to display and attract females, which is basically dependent on body condition, should be high. As pointed out by Carranza and Hidalgo (1993), this is not surprising in a long-lived species like the great bustard (up to 30 years recorded by Gewalt 1959, for a captive bird; maximum survival recorded in free-living individuals, 15 years, personal observation) in which sexual maturity is not reached until the age of 3–5 years (Gewalt 1959; Cramp and Simmons 1980; Morales 1999). Nevertheless, females might to some extent be evaluating male age through an epigamic trait like neck development, since age is itself a viability indicator (Trivers 1972; Halliday 1983; Manning 1985, 1989), which can be reflected in the degree of development of secondary sexual traits (Manning 1985) and has already been identified in several polygynous bird species (Davison 1981; Smith 1982; Manning 1985, 1989).

In conclusion, the results of the present study seem to support the role of body condition as a fundamental factor determining the capacity of great bustard males to afford the costs of sexual activity, which is in agreement with the association between body condition and epigamic traits of great bustard males found in a previous work on captive birds by Carranza and Hidalgo (1993). That study, however, did not account for individual differences in display rate, and thus the effect of body condition on the sexual activity of free-living individuals could not be directly assessed. Body condition seems to determine male attractiveness and therefore potential mating success in male great bustards.

This result is also consistent with those found in other studies on different polygynous and lekking species (Payne 1984; Clutton-Brock 1988; Andersson 1994). The role of age could not be unambiguously established, although phenotype may function as an age indicator, thus helping females evaluate male viability. These conclusions support a total viability scenario (Manning 1985) in which the advertisement of global fitness is based on condition-dependent phenotypic and behavioural traits.

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## References

- Alonso JC, Alonso JA (1996) The great bustard (*Otis tarda*) in Spain: present status, recent trends and an evaluation of earlier censuses. *Biol Conserv* 77:79–86
- Alonso JC, Alonso JA, Martín E, Morales MB (1995) La avutarda en la Reserva de Las Lagunas de Villafáfila. Instituto de Estudios Zamoranos Florian de Ocampo (CSIC) – Fundación para la Ecología y la Protección del Medio Ambiente, Zamora, Spain
- Alonso JC, Alonso JA, Morales MB, Martín E (1996) Seasonal and interannual population dynamics of the great bustard (*Otis tarda*) at Villafáfila Reserve, NW Spain. In: Fernández Gutiérrez J, Sanz-Zuasti J (eds) Conservación de las aves esteparias y su hábitat. Junta de Castilla y León, Valladolid, Spain, pp 191–200
- Andersson M (1986) Evolution of condition-dependent sex ornaments based on viability differences. *Evolution* 40:804–816
- Andersson M (1994) Sexual selection. (Monographs in ecology and behaviour) Princeton University Press, Princeton, N.J.
- Andersson S (1992) Female preference for long tails in lekking Jackson's widowbirds: experimental evidence. *Anim Behav* 43:379–388
- Badyaev AV, Etjes WJ, Faust JD, Martin TE (1998) Fitness correlates of spur length and spur asymmetry in male wild turkeys. *J Anim Ecol* 67:854–852
- Brown ME (1996) Assessing body condition in birds. *Curr Ornithol* 13:67–121
- Carranza J, Hidalgo SJ (1993) Condition-dependence and sex traits in the male great bustard. *Ethology* 94:187–200
- Clutton-Brock TH (1988) Reproductive success. University of Chicago Press, Chicago
- Cramp SK, Simmons EL (1980) The birds of the western Palearctic, vol 2. Oxford University Press, Oxford
- Darwin C (1871) The descent of man and selection in relation to sex. Murray, London
- Davison GWH (1981) Sexual selection and the mating system of *Argusianus argus* (Aves: Phasianidae). *Biol J Linn Soc* 15:91–104
- Fiske P, Kålås JA (1995) Mate sampling and copulating behaviour of great snipe females. *Anim Behav* 49:209–219
- Folstad I, Karter AJ (1992) Parasites, bright males, and the immunocompetence handicap. *Am Nat* 139:603–622
- Gewalt W (1959) Die Großtrappe. Die Neue Brehm-Bücherei, Wittenberg-Lutherstadt, Germany
- Gibson RM (1996) Female choice in sage grouse: the roles of attraction and active comparison. *Behav Ecol Sociobiol* 39:55–59
- Gilliard ET (1969) Birds of paradise and bowerbirds. Weidenfeld & Nicholson, London
- Glutz, UN, Bauer KM, Bezzel E (1973) Handbuch der Vögel Mitteleuropas, vol 5. Akademische Verlagsgesellschaft, Frankfurt am Main, Germany
- Halliday TR (1983) The study of mate choice. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, pp 3–32
- Hellmich J (1991) La avutarda en Extremadura. Monografías Alytes-Adenex, Mérida, Spain
- Hidalgo SJ, Carranza J (1990) Ecología y comportamiento de la avutarda (*Otis tarda*). Universidad de Extremadura, Cáceres, Spain
- Hidalgo SJ, Carranza J (1991) Timing, structure and functions of the courtship display in male great bustard. *Ornis Scand* 22:360–366
- Höglund J, Alatalo R (1995) Leks. Princeton University Press, Princeton, N.J.
- Höglund J, Robertson JGM (1990) Spacing of leks in relation to female home ranges, habitat requirements and male attractiveness in the great snipe (*Gallinago media*). *Behav Ecol Sociobiol* 26:173–180
- Jiguet F (2001) Defense des Ressources, Choix du Partenaire et Mécanismes de Formation des Leks chez l'Outarde Canepetière. Thèse de Doctorat, Université de Paris 6, Paris
- Kirkpatrick M, Ryan MJ (1991) The evolution of mating preferences and the paradox of the lek. *Nature* 350:33–38
- Kodric-Brown A, Brown JH (1984) Truth in advertising: the kind of traits favoured by sexual selection. *Am Nat* 124:309–323
- Manning JT (1985) Choosy females and correlates of male age. *J Theor Biol* 116:349–354
- Manning JT (1989) Age-advertisement and the evolution of the peacock's train. *J Evol Biol* 2:379–384
- Martin P, Bateson P (1993) Measuring behaviour. An introductory guide, 2nd edn. Cambridge University Press, Cambridge
- Martínez C (2000) Daily activity patterns of great bustards *Otis tarda*. *Ardeola* 47:57–68
- Maynard-Smith JM (1991) Theories of sexual selection. *Trends Ecol Evol* 6:146–151
- Morales MB (1999) Ecología reproductiva y movimientos estacionales en la avutarda (*Otis tarda*). Tesis doctoral, Universidad Complutense de Madrid, Madrid
- Morales MB, Jiguet F, Arroyo B (2001) Exploded leks: what bustards can teach us. *Ardeola* 48:85–98
- Payne RB (1984) Sexual selection, lek and arena behavior and sexual size dimorphism in birds. *Ornithol Monogr* 33
- Reynolds JD, Gross MR (1990) Costs and benefits of female mate choice: is there a lek paradox? *Am Nat* 136:230–243
- Rintamäki PT, Alatalo RV, Höglund J, Lundberg A (1995a) Mate sampling behaviour of black grouse females (*Tetrao tetrix*). *Behav Ecol Sociobiol* 37:209–215
- Rintamäki PT, Alatalo RV, Höglund J, Lundberg A (1995b) Male territoriality and female choice on black grouse leks. *Anim Behav* 49:759–767
- Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences, 2nd edn. McGraw-Hill, New York
- Smith LH (1982) Moulting sequences in the development of the tail plumage of the superb lyrebird *Menura novaehollandiae*. *Aust Wild Res* 9:311–330
- Sokal RR, Rohlf FJ (1969) Biometry. Freeman, New York
- Statsoft Inc. (1998) Statistica for Windows version 5.1 user manual. Statsoft Inc., Tulsa, Okla.
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man, 1871–1971. Heinemann, London, pp 136–179
- Vehrencamp SL, Bradbury JW, Gibson RM (1989) The energetic cost of display in male sage grouse. *Anim Behav* 38:885–896
- West-Eberhard MJ (1979) Sexual selection, social competition, and evolution. *Proc Am Philos Soc* 123:222–234
- Williams GC (1966) Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton, N.J.