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Otis tarda Great Bustard

Du. Grote Trap Fr. Outarde barbue Ge. Großtrappe It. Otarda
Ru. Дрофа Sp. Avutarda Común Sw. Stortrapp

Otis tarda Linnaeus, 1758

Polytypic. Nominate *tarda* Linnaeus, 1758, Iberia, Morocco, Turkey, and central and south-east Europe, east to central Siberia in upper basin of River Irtysh. Extralimital: *dybowskii* Taczanowski, 1874, east Asia, from the eastern Altai and Lake Baikal to northern China.

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Summary. The sections on Field characters, Habitat, Distribution, Population, Movements, Food, Social pattern and behaviour, Breeding, Plumage, Measurements, Weights, and Geographical variation have been updated and partially re-written. Two new sections have been created on Conservation and Survival. New information is given on age and timing of acquisition of full adult plumage, habitat use in Iberia, changes of range and population numbers in most European countries, seasonal movements and migration in Iberia, central Europe, Russia and Turkey, as well as juvenile dispersal, diet composition in Spanish populations, organization of mating system, correlates of display rate and male mating success, timing of breeding, nesting substrate, clutch size in Iberia and Hungary, weather correlates of population productivity, individual correlates of female breeding success, parental care, and chick independence timing. Additionally, new measurements and weights of captured free-living juvenile and adult birds are provided, as well as recent results on phylogeography in Europe, based on mitochondrial DNA. The Survival and Conservation sections respectively, describe juvenile and adult survival rates and longevity in different Spanish regions, and summarize the main threats and management priorities for the species.

Field characters. (Updates *BWP* Vol. II, p. 659) See Fig. 1.

Juvenile. Male acquires full adult plumage and size between third and sixth summers.

Habitat. (Updates *BWP* Vol. II, pp. 659–60)

Across middle latitudes, especially in steppe zone, but penetrating into temperate, Mediterranean, and marginally into boreal and oceanic zones. Strongly attached to lowlands, river valleys, and undulating open country, avoiding steep or rocky terrain, deserts, wetlands, forests, and savannas or parklands with more than isolated or small clumps of trees (though, at least in Iberian Peninsula, uses open oak woodland and olive groves). Also avoids areas liable to annual rainfall much above 600 mm. Tolerates cold, but heavy or prolonged snow cover may be cause of regular or irregular migrational status in some areas. In Russian Federation, nest locally up to *c.* 3000 m, and winters up to 2000 m (Dementiev and Gladkov 1951). Soil types used by Hungarian population (Sterbetz 1977) have low-lying water-table promoting low humidity and warm microclimate (as do those of east European steppes). Additionally, dried-up peat-fen soils freely used. Low moisture levels serve to discourage invasion by pioneer trees, while encouraging growth of herbage tall enough to provide ample food and partial cover. Prior to human intervention, species presumably confined to natural grassy steppes and similar warm open habitats. Advent of man pushed forest-edge northwards and created extensive arable fields bearing crops such as rape,

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Fig. 1. *Otis tarda* Great Bustard: **1** and **2** adult male breeding; **3** and **4** adult female breeding; **5** adult male non-breeding; **6** adult female non-breeding; **7** 1st summer male; **8** juvenile male; **9** downy young. Artist: John Davis.

kale, wheat, barley, and later alfalfa, which seem often to have proved more attractive than natural habitats, particularly in areas with high diversity of low-intensity land use and no human disturbance, as well as low density of buildings and infrastructure (Sterbetz 1977, Alonso and Alonso 1990, Lane *et al.* 2001, Osborne *et al.* 2001). A clear view over 1 km or more on at least three sides apparently essential, as well as uninterrupted mobility in all directions on ground. Prefers naturally well-drained but moist soils, carrying short or medium herbage or crops, and, for breeding, somewhat taller growth such as winter-sown rye or other cereals, *Molinia* grasslands, meadows, or semi-arid sagebrush, especially where ready access to ample and diverse food resources.

Distribution. (Replaces *BWP* Vol. II, pp. 660–1) See Fig. 2.

Range increased markedly in western and central Europe, with clearance of forest areas probably reaching maximum extension towards end 18th century, then began to retreat as steppes and dry meadows replaced by arable (see map and land use statistics in Isakov 1974; also Kirikov 1960). Range now severely fragmented due to further habitat changes caused by e.g. mechanized farming and possibly pesticides together with excessive hunting pressures (Glutz von Blotzheim *et al.* 1973, Sterbetz 1975, 1977; see also Habitat).

Britain. Extinct. Formerly bred many parts of England; also south-east Scotland before 1526. Last bred Norfolk 1830 and Suffolk 1832 (British Ornithologists' Union 1971). Sweden. Rare breeder in south until mid-19th century. Denmark. Bred once, 1860 (Salomonsen 1963). France. Formerly bred, especially Champagne and Vendée, but extinct after 1863 (Yeatman 1971). Netherlands. No successful breeding but infertile eggs laid by unpaired females between 1914 and 1918, and in 1947 and 1948 (Glutz von Blotzheim *et al.* 1973). Germany. Extinct in western part. Bred in Niedersachsen up to 1885 and Holstein until 1910 (Glutz von Blotzheim *et al.* 1973). Poland. 592 birds in 1936, *c.* 430 in 1959, *c.* 305 in 1963 (Tomialojc, 1972). Rapid decline 1970s and early 1980s; extinct since 1986 (*BWP* Concise Edition Vol. 1). Switzerland. Bred 1553 (Glutz von Blotzheim *et al.* 1973). Greece. Formerly bred in north and central Greece but extinct end 19th century (Bauer *et al.* 1969, Glutz von Blotzheim *et al.* 1973). Moldova. Practically extinct (see Population). Azerbaijan. Bred until 1940s–50s. Syria. Breeding in north; last proved 1931 (Kumerloeve 1968); doubtful if still breeds. Iraq. Has bred in north (Moore and Boswell 1956); no recent records, but population likely to be small if still extant.

Breeds in Spain, Portugal, eastern Germany, Czech Republic, Slovakia, Hungary, Austria, former Yugoslavia,

Fig. 2. *Otis tarda* Great Bustard distribution within west Palearctic: red = migrant breeding; brown =resident breeding; green = normal winter. Reprinted from the Concise Edition of *BWP* with amendments for Iberia, Hungary, and Turkey.

Rumania, Bulgaria, Turkey, Ukraine, Russian Federation, and Morocco (see Population).

Accidental. Britain, Ireland, Finland, Norway (only 18th century), Sweden, Denmark, France, Belgium, Netherlands, Luxembourg, Poland, Switzerland, Italy, Malta, Albania, Greece, Belarus, Lithuania, Latvia, Estonia, Algeria, Tunisia, Egypt (Atta 1992), Lebanon, and Israel.

Beyond west Palearctic, extends (very discontinuously) east through central Asia to north-east China and southern Ussuriland; also breeds in Iran.

Population. (Replaces *BWP* Vol. II, p. 661)

The distribution map (Fig. 2) has been updated for Iberia, Hungary, and Turkey.

SPAIN. Largest population of western Palearctic. Estimated 16 000–17 000 birds 1969 (Trigo de Yarto 1971*a*, *b*), although lower (more realistic) numbers provided later: 11 890 birds 1975 (Palacios *et al.* 1975), 11 282 birds 1980 (De la Peña 1980), 6000–8000 birds 1981 (Garzón 1981), 8000–9000 birds 1982 (Purroy 1982), 5000–8000 birds 1985 (Collar 1985). Higher estimates in 1990s, with 11 500 (Hidalgo de Trucios 1990), 13 500–14 000 birds 1990 (Alonso and Alonso 1990), and 17 000–19 000 birds 1996 (Alonso and Alonso 1996) as most accurate, thus showing no clear overall trend in *c.* 30 years. Mainly concentrated in central plateaux and Extramadura, with peripheral populations in Ebro and Guadalquivir valleys (Alonso and Alonso 1996). Northern plateau holds *c.* 10 000 birds (ETI 1998), southern plateau4182–4432 birds (Hernández *et al.* 1987, Alonso and Alonso 1996, Palacín *et al.* 1996, Martín *et al.* 1999), Extremadura 5500–6500 birds (Hellmich 1994, Sánchez *et al.* 1994, Alonso and Alonso 1996), Ebro Valley *c.* 95 birds (Elósegui 1985, Cabrera *et al.* 1987, Alonso and Alonso 1996), and Andalucía *c.* 200 birds (Lane and Alonso 2001), which gives total of 19 977–21 227. Recent revision estimates up to 23 000 (Alonso *et al.* 2002). PORTUGAL. Between 650 (counted) and 1000 (estimated maximum) 1977 (*BWP* Vol. II, pp. 659–68), 500–700 birds early 1990s (Tucker and Heath 1994) in central-eastern (continuing with Spanish populations) and southern parts of country (Alentejo region, holding >90% of population; Rocha and Moreira 1999). Actual estimate 1000–1100 birds (F Moreira). GERMANY. Estimated 4100 birds in 1940, 1200 in 1960, 560 birds in 1980, reduced to 220 by 1990 and 90–100 birds in 1995 (Litzbarski and Litzbarski 1996). CZECH REPUBLIC. 10–20 individuals in 1995 confined to southern Moravia (Kollar 1996). SLOVAKIA. Estimated 2400 birds in 1900, 1160 birds in 1695, and 550 in 1973 (Randik 1978). 20–30 birds estimated in early 1990s (Kollar 1996). Current estimate 5–10 in south, near border with Austria and Hungary (J Chavco and S Vongrej), although last observed nesting in 1994, close to Austrian border (J Chavco and S Siryová). Regular wintering of 20–90 birds close to Austrian and Hungarian border, supposedly coming from those countries (J Chavco and S Siryová). HUNGARY. Estimated 8557 birds 1941, 2360 birds 1969, 3200–3200 birds 1973 (Fodor 1973–4, Sterbetz 1975), and 3237 birds 1977 (I Sterbetz). Only five main populations remaining during 1980s and 1990s (Faragó 1993) in north-western (close to Austrian border), central, and eastern Hungary (limiting with Rumanian and Yugoslavian borders). Decline continued during those years, with 2294 birds 1981, 2691 birds 1985, 1594 birds 1988, 1363 birds 1990, and 1100–1300 birds 1995 (Faragó 1993, 1996). AUSTRIA. Continuous population and range reduction, with extinction of peripheral nuclei; estimates of 700–800 birds in 1939–40, *c.* 400 birds 1958, 200–230 birds 1969–72, 150–170 birds 1975, and 110–120 birds 1977 (Glutz von Blotzheim *et al.* 1973, Lütkens and Dangel 1975, Lütkens and Eder 1977; M Walgram). Four small populations left in 1978 in plains close to Vienna and to Slovakian and Hungarian borders (Marchfeld, *c.* 25 birds; Weinviertel, *c.* 25 birds; Hanság, *c.* 57 birds; Parndorfer Platte, *c.* 14 birds). Further reduction recorded in 1988 (Marchfeld,24 birds; Weinviertel, *c.* 18 birds; Hanság, 16 birds; Parndorfer Platte, 5 birds), and some stabilization in 1994 (Marchfeld, 15 birds; Weinviertel, 23 birds; Hanság, *c.* 18 birds; Parndorfer Platte, *c.* 5 birds) (Kollar and Wurm 1996). FORMER YUGOSLAVIA. Kollar (1996) reported 8–10 birds still breeding close to Hungarian border (Vojvodina). RUMANIA. Marked decline from 1110 birds 1955, to 313 birds 1975, and 296 birds 1976 (Fodor 1977). Nearly extinct in 1990s with only 10–15 birds left (Kollar 1996). BULGARIA. 180–200 birds 1918–39, 35–40 birds 1967–8, apparently none breeding 1976 (Fodor 1977), 10–15 birds in early 1990s (Kollar 1996). Wintering of up to total of 2000 birds, probably coming from Russia, 1970–85. MOLDOVA. 2–3 birds recorded 1988 (Tucker and Heath 1994), now probably extinct. TURKEY. Marked decline since 1930s (H Kumerloeve), estimated 800–3000 birds 1990s (Kollar 1996). Actual estimates 3000–6000 breeding birds (Eken and Magnin 2000). Decline continues, especially in west. Most important populations remain in central (Tuz Gölü basin) and eastern Turkey where numbers larger than expected (Eken and Magnin 2000). UKRAINE. 300–400 breeding birds 1995 (Kollar 1996), but receives important wintering population from Russia (e.g. 7246–8096 birds in south Ukraine during winter 1998–9; Andryushchenko *et al.* 2000). RUSSIAN FEDERATION. Maximum range and population at end 18th century when spread north into steppe areas after forest clearing; marked decline in 19th century with cultivation of steppes and meadows, which has continued, until in 1971 only 2200–2300 breeding 'pairs' of nominate *tarda* (*c.* 7000 birds including subadults) and 500–600 'pairs' of eastern race *dybowskii* (Kirikov 1960, Isakov 1974). Not less than 8000 birds in whole country in 1991 (Flint and Mishchencko 1991). *c.* 8000 birds in European Russia, 6000 of which breed in Saratov region, in Volga basin (Antonchikov 1998, 2000). No clear trend to increase since 1970s (Antonchikov 2000). MOROCCO. Declining despite protection; confined to north-west where 90–133 birds in 1998–9 (Hellmich 1999, Alonso *et al.* 2000*a*). In summary, *c.* 40 000 birds present in western Palearctic.

Conservation. (New section)

Globally threatened species listed as 'vulnerable' in *Threatened Birds of the World* (BirdLife International 2000) and SPEC 1 in Europe (Tucker and Heath 1994). Main threats are habitat loss and degradation leading to fragmentation through agricultural intensification involving crop spraying or irrigation and intrusion of mechanical vehicles, ploughing of grasslands, afforestation, intensive grazing, installation of fences, ditches, and hedges, and construction of new infrastructures such as roads and powerlines. High mortality among eggs and chicks by predation, mainly corvids on eggs, and harriers (*Circus pygargus* and *C. cyaneus*), foxes (*Vulpes vulpes*), and feral dogs on chicks (Ena *et al.* 1987; B Arroyo), human disturbance during agricultural works and food shortage produced by the use of pesticides and fertilizers. Significant level of mortality from collisions with powerlines since species is mainly terrestrial. Flies (except on migration) below 200 m, normally *c.* 30–100 m, with limited powers of aerial manoeuvre, and consequently very vulnerable to such hazards (Alonso *et al.* 1994, Alonso and Alonso 1999, Martín 2001). Poaching is still problem in parts of range (e.g. Spain, Turkey, and Ukraine) and disturbance during hunting of legitimate game is also important (Kollar 1996). Modelling of extinction likelihood of small and fragmented populations shows that probability of extinction in 100 years may be close to 100% if habitat and populations are not properly managed (Lane and Alonso 2001). Habitat selection and genetic studies suggest limited colonization capacity due to strong fidelity to breeding and natal sites (Lane *et al.* 2001, Martín *et al.* 2002; see Movements). Genetic studies based on distribution of mitochondrial haplotypes suggest that high female fidelity to natal sites leads to demographic independence even among populations separated by only *c.* 50 km. These local populations are genetically connected only by male natal dispersal and should be considered different management units (Martín *et al.* 2002).

Conservation priorities involve implementation of agri-environmental measures (e.g. increasing alfalfa and rape cultivation, regulation of livestock densities, regulation of crop spraying, adaptation of agricultural activities to species life cycle) to maintain open areas of non-intensive farmland, protect and manage existing display and breeding areas (given limited recolonization capacity), prevent disturbance (e.g. increase wardening), ensure availability of winter habitat, reduce adult mortality by preventing illegal hunting and collision with powerlines, research on limiting factors, increase international cooperation, and develop public awareness campaigns (Kollar 1996). Captive breeding programmes need improvement to be effective (Martín *et al.* 1996), and re-introduction programme with Russian birds currently being prepared in England.

Movements. (Replaces *BWP* Vol. II, pp. 661–2)

Migratory in east, dispersive or resident elsewhere. Telemetry studies revealed that movements in Iberia more important than previously thought. Most males leave breeding grounds after mating season, flying up to 167 km to summering–wintering areas, normally showing interannual fidelity to both breeding and summering–wintering areas (Morales *et al.* 2000, Alonso *et al.* 2001). Some females travel to wintering grounds up to 100 km distant (Alonso *et al.* 2000*b*, Martín 2001). Young males undertake longer juvenile dispersal than females, reaching maximum distances of 188 and 132 km, respectively (Alonso *et al.* 1998, Martín 2001). Males settle as adults at leks located up to >100 km away from natal site, while females normally return to natal site to breed after juvenile dispersal (Alonso *et al.* 1998, Martín 2001).

In central Europe, basically resident or locally dispersive in mild, snow-free winters, but in severe winters northern flocks in particular liable to be displaced over several hundred kilometres (Gewalt 1959). May disperse regularly away from hilly parts of Slovakia (Ferianc 1963); formerly in Austria, where, however, has taken to overwintering in last 50 years, following widespread cultivation of oil-seed rape *Brassica napus* (Ferguson-Lees 1966). Successful overwintering in favourable area can soon lead to its becoming traditional winter haunt (Glutz von Blotzheim *et al.* 1973), thus now winters regularly in some numbers in Hanság region on frontiers of Hungary and Austria (Lukschanderl 1971); such birds have not necessarily travelled long distances. Cold-weather movements most marked in eastern and northern Europe, as reported for Hungary, where in winters 1969–70, 1978–9, 1984–5, and 1986–7, most birds of Carpathian basin moved principally south or south-west to Yugoslavia, Greece, and mainly to Italy (Faragó 1990). Birds apparently more reluctant to migrate after January, despite snowfall, due to proximity of mating season (Faragó 1990). In eastern Germany, birds move west, some as far as North Sea countries. Recent invasion in winters 1962–3 and 1969–70. During latter, *c.* 300 birds reached western Germany, Netherlands, and Belgium (with *c.* 10% mortality there), a few individuals occurring south-west to Bavaria and France and north-west to Denmark and Britain (Dornbusch 1982, 1987); western influx late December and January, return eastwards in March (Hummel and Berndt 1971). Although cold-weather migration initially thought not to be directly correlated with snow cover (Hummel and Berndt 1971, Glutz von Blotzheim *et al.* 1973), found that this is much stronger trigger for migration than frost and low temperatures (J Streich).

Birds breeding in Ukraine resident (Dementiev and Gladkov 1951). In contrast, in Russia truly migratory, wintering in southern Ukraine as shown by satellite telemetry (Watzke *et al.* 2001), while 1000–4000 birds winter in Russian Caucasia (Stavropol region, Hohkov 1998). Small numbers remain in breeding grounds near Saratov (A Antonchikov). Turkey may receive a few wintering birds from Russia that remain near Black Sea coast. Most Turkish breeding birds perform dispersive seasonal movements within country, so that winter presence of foreign birds is very small. However, part of population breeding on eastern plateau (average altitude 2000 m above sea level) leaves breeding grounds, probably wintering in Syria, Iraq, and Iran (Eken and Magnin 2000).

Autumn migration protracted; in northern parts of Russian Federation, some birds (probably inmmatures) start moving in August while others stay until heavy snow covers ground; main passages early October to mid-December. Spring return begins early, and proceeds more quickly than autumn exodus. Northwards movement through Ukraine and Transcaucasia from early March (peak mid-March), and winter flocks gone from southern steppes by end March or early April; breeding grounds re-occupied by mid-April.

Food. (Updates *BWP* Vol. II, pp. 662–3)

Spanish birds possibly take more wild vegetation and fewer vertebrates than central and eastern European populations; in spring, average volumetric percentages per stomach gave ratio of 10 : 1 plant : animal material, most favoured plants being *Taraxacum*, *Hypochaeris*, *Plantago*, *Podospermum*, *Medicago*, *Thrincia*, *Diplotaxis*, *Brassica*, *Leucanthemum*, *Vicia*, *Trifolium*, *Aegylops*, *Vulpia*, *Hedypnois*, *Ornithopus*, and *Scorpiurus*. Coleoptera form 95% of insect prey numbers, especially *Tropinota* (Scarabaeidae), *Brachycerus* (Curculionidae), *Pimelia*, *Sepidium* (Tenebrionidae), and Meloidae. Orthoptera important in late spring. In summer, green plant foods replaced by cereal seeds, Mantidae, Orthoptera (Tettigoniidae, Acrididae), and ants (Formicidae). In autumn, diet similar though increase in seeds of cultivated species. In winter, reverts to green plants (Compositae, Gramineae, Leguminosae, and Salsolaceae) with seeds of cultivated species (wheat, grape, lentil, olive) still important, and insects almost absent (Palacios *et al.* 1975, Lane *et al.* 1999). Evidence, from the few stomach analyses and observations, suggests that this general seasonal pattern followed elsewhere in Europe, i.e. diet mainly animal (especially insects) in summer, mainly plant in winter, spring, and autumn (for details, see Dementiev and Gladkov 1951, Nečas and Hanzl 1956, Gewalt 1959, Fodor *et al.* 1971, Glutz von Blotzheim *et al.* 1973). In spring, Portugal, marked preference shown for salad mustard *Eruca vesicaria* (N J Collar). Occasionally damage to winter crops caused, though insect and rodent pests may be taken in great quantities (Gewalt 1959). In Spanish northern plateau, dry-cultivated alfalfa *Medicago sativa* strongly selected throughout year, but grasses used less often than expected from availability. Positive selection of Coleoptera, no clear selection of Orthoptera or Hymenoptera (Lane *et al.* 1999).

Social pattern and behaviour. (Upadtes *BWP* Vol. II, pp. 663–5)

1. Highly gregarious for much of the year, forming social units (or 'droves') often comprised largely of birds of same sex but varying ages (Hidalgo de Trucios and Carranza 1990, Alonso *et al.* 1995). When resident on ancestral habitat, as mainly in Europe, whole local populations may sometimes unite in single loose flock in winter; especially when weather hard, may wander and congregate with other flocks—numbers then formerly up to several thousands in places, but maximum now in order of only 100–200 (Glutz von Blotzheim *et al.* 1973). Within same flock, sexes normally keep distinct. General groupings into droves of females and first-year birds occur in autumn, gradually integrating into larger flocks.

BONDS. Mating system polygynous and promiscuous, linked with skewed sex ratio and sexual maturation at different ages in males and females. Data on sex ratio showing surplus of breeding females of up to 2.5 : 1 after Glutz von Blotzheim *et al.* (1973), but even higher in Morocco (3.3 : 1 during breeding season; Alonso *et al.* 2000*a*). In north-west Spain, 1.72 : 1 during breeding season, up to 2.79 : 1 in summer, and 2.91 in autumn–winter (Alonso *et al.* 1996), where variations due to seasonal movements (Alonso *et al.* 1996, Morgado and Moreira 2000, Martín 2001). Sexual maturity earlier in females: age of first reproductive attempt 2 years (Morales *et al.* 2002*a*). Males do not mate successfully until probably 5–6 years: number of copulation attempts significantly greater among tagged males older than 6 years in north-west Spain, although also recorded among 3- to 6-year-olds (Morales 1999). Mating skew probably considerably higher (Morales 1999). Males with better body condition (weight/tarsus length) and longer moustache feathers presented significantly higher sexual display rate, and those displaying at higher rate both attracted more females and performed more copulation attempts (Morales *et al.* 2002*a*, *b*). No evidence in Europe of monogamous pair bond, as asserted by E P Spangenberger in Dementiev and Gladkov (1951) and Sterbetz (1981). Lek-like mating systems, either classical and/or exploded (displaying males less clumped than in classical leks and aggregation not normally detected until males mapped over large area; males hold and patrol larger territories which may be used by females to forage and even nest, but whose resource content—food, shelter—is not decisive in female choice, basically based on male phenotype; Lewis 1985, Höglund and Alatalo 1995, Ligon 1999; Table 1), most extended (*BWP* Vol. II, p. 663; Gewalt 1959, Carranza *et al.* 1989, Hidalgo de Trucios and Carranza 1990, Morales *et al.* 1996, Morales 1999, Morgado and Moreira 2000), although polygyny (resource and/or harem based) also described (Sterbetz 1981, Carranza *et al.* 1989, Hidalgo de Trucios and Carranza 1990), as well as isolated promiscuity (Sterbetz 1981). Under both lekking and polgyny, but more obviously in latter, females establish social rank-order (*BWP* Vol. II, p. 663); males also show similar dominance hierarchy (*BWP* Vol. II, p. 663; Hidalgo de Trucios and Carranza 1991). Role of male restricted to attraction and fertilization of females, since only females tend young. Female maintains strong bond with offspring, which lasts through winter and up to next breeding season, even after families combine in larger flocks (Martín 1997, Alonso *et al.* 1998). Yearlings may sometimes remain with mother beyond new breeding season (Martín 1997).

BREEDING DISPERSION. Based on observations in north-west Spain (Morales 1999, Alonso *et al.* 2000*b*): males undergo significant variation in aggregation level during mating season, starting display in large, compact flocks (March) and ending up strutting solitarily, but normally within sight of each other, and disperse over large area (exploded lek). Mating peak reached during dispersal phase, normally second week of April. Males do not hold exclusive territories, but largely overlap without fixed display stations (mobile lek). Home-range of females during mating season noticeably larger than that of males (J C Alonso and M B Morales). Similar behaviour observed in other parts of Spain, e.g. Madrid (J C Alonso and C A Martín) and Extremadura (Hidalgo de Trucios and Carranza 1990), and in Portugal (*BWP* Vol. II, p. 663). In latter two sites, polygamous territorialism also described, although not clear whether resource or harem based (Morales *et al.* 2001). Lek arenas used over many years (Morales *et al.* 2000). Minority of males holding mating territories (see above) defend indistinct area from intrusion by other males, though female members of

Table 1. Mating system assessment in *Otis tarda* Great Bustard: several stages have been proposed in a gradient ranging from classical leks to monogamy

Mating system	Description	References
Classical lek	Clumped aggregation of males visited by females for copulation only	*BWP* Vol. II, pp. 663; Gewalt 1959, Carranza *et al.* 1989
Exploded lek	Loose aggregation of males where females copulate, but may also feed and/or nest; female choice not linked to territory quality	Hidalgo de Trucios and Carranza 1990, Morales *et al.* 1996, Morales 1999
Resource-based polygyny	No aggregation; females select territory mainly based on quality	Carranza *et al.* 1989, Hidalgo de Trucios and Carranza 1990
Harem-based polygyny	No aggregation; females actively defended by males	Sterbetz 1981, Carranza *et al.* 1989, Hidalgo de Trucios and Carranza 1990
Isolated promiscuity	No aggregation; no female territory dependence or defence	Sterbetz 1981
Monogamy	Stable male–female bond	Sterbetz 1981

Based on Morales *et al.* (2001) and reproduced with permission of SEO-Birdlife.

harem often range beyond it and exclusiveness of territory partly effected by simply remaining at some distance from chief display-ground (*BWP* Vol. II, p. 663). After mating, females disperse to nest and do not usually return to mating area. Nests solitary, scattered around central display-ground, often relatively close to display-stations of males, and within their home-ranges (*BWP* Vol. II, p. 663; Alonso *et al.* 2000*b*, Morgado and Moreira 2000), but may be at considerable distances (>10 km; *BWP* Vol. II, p. 663; Alonso *et al.* 2000*b*). Once established, nest areas normally used every year (Gewalt 1959, Alonso *et al.* 2000*b*). Nests of neighbouring females sometimes close enough for birds to associate during feeding breaks. Several nests may be found in single field (CAM): up to 4 as reported by Verner (1909) in Spain. In Portuguese hay crop, 4 nests within diameter of 200 m and 2 only 58 m apart. In Slovakia, nests in formerly densely populated areas as close as 60–80 m at times (Nečas and Hanzl 1956). Up to 20–30 or more immature males may form highly excitable, close droves in spring (Hidalgo de Trucios and Carranza 1990); throughout breeding season, tend to remain separate from adults and most central display-ground, though stay within ancestral terrain (*BWP* Vol. II, p. 663; Morales 1999).

Roosting. At night both solitary and gregarious; on ground. Tends to sleep at whatever spot reached when darkness falls, though will make for vantage points (ridges, knolls) and, in breeding season, mature males usually return to same site to roost (solitarily). Active into darkness. Some nocturnal activity in spring: grunts of disputing males heard in pitch dark before dawn (*BWP* Vol. II, p. 663) and display witnessed by moonlight (Gewalt 1959). Daytime roosting occurs regularly in spring and summer at variable length, particularly on very hot days, generally 11.00–17.00 hrs (Morales 1999, Martínez 2000).

2. In breeding season, behaviour particularly characterized by extraordinarily elaborate Balloon-display of adult males; this essentially visual, apparently unimportant 'timpano' sounds produced when male inflates and deflates gular pouch (see Bare parts and Structure for seasonal changes) audible only at relatively close range, carrying *c.* 50 m in still conditions, and seems merely incidental (*BWP* Vol. II, p. 663; Glutz von Blotzheim *et al.* 1973). Display described in great detail by Glutz von Blotzheim *et al.* (1973), but also by Hidalgo de Trucios and Carranza (1990) and Hellmich (1991). Starts with all-male droves from late winter onwards (Hidalgo de Trucios and Carranza 1991), but most frequent on display-grounds later. Sexual readiness of males signified by amount of white plumage displayed, although Balloon-displays in male droves in late winter and early spring more linked to establishment of male hierarchy than to female attraction (Hidalgo de Trucios and Carranza 1991). Display duration longer in small flocks or solitary males, as importance for female attraction increases as mating peak approaches (Hidalgo de Trucios and Carranza 1991, Morales 1999).

Display-ground Behaviour. Both sexes present on or near traditional display-grounds during late winter (from late January to mid-March; Morales *et al.* 2000) and spring, but male display from dispersed stations within area does not begin until mid-March in eastern Germany (Gewalt 1959), and *c.* early April in central and north-west Spain (Morales 1999; C A Martín and J C Alonso). Isolated males also display in same manner within own mating territories elsewhere (see above). Main period of activity on display-grounds from late March to end April (correlated with nesting peak in mid-May) but some display may continue until early June (correlated with replacement layings); exceptionally, July–November (Glutz von Blotzheim *et al.* 1973). Activity mostly in early morning (daybreak to *c.* 08.00 hrs) and late afternoon (17.00 hrs until dark; Morales 1999, Martínez 2000); on moonlit night observed towards midnight and at 03.00 hrs. Disposition to display indicated by characteristic springtime carriage of tail in sharp upright position, exposing elevated white under

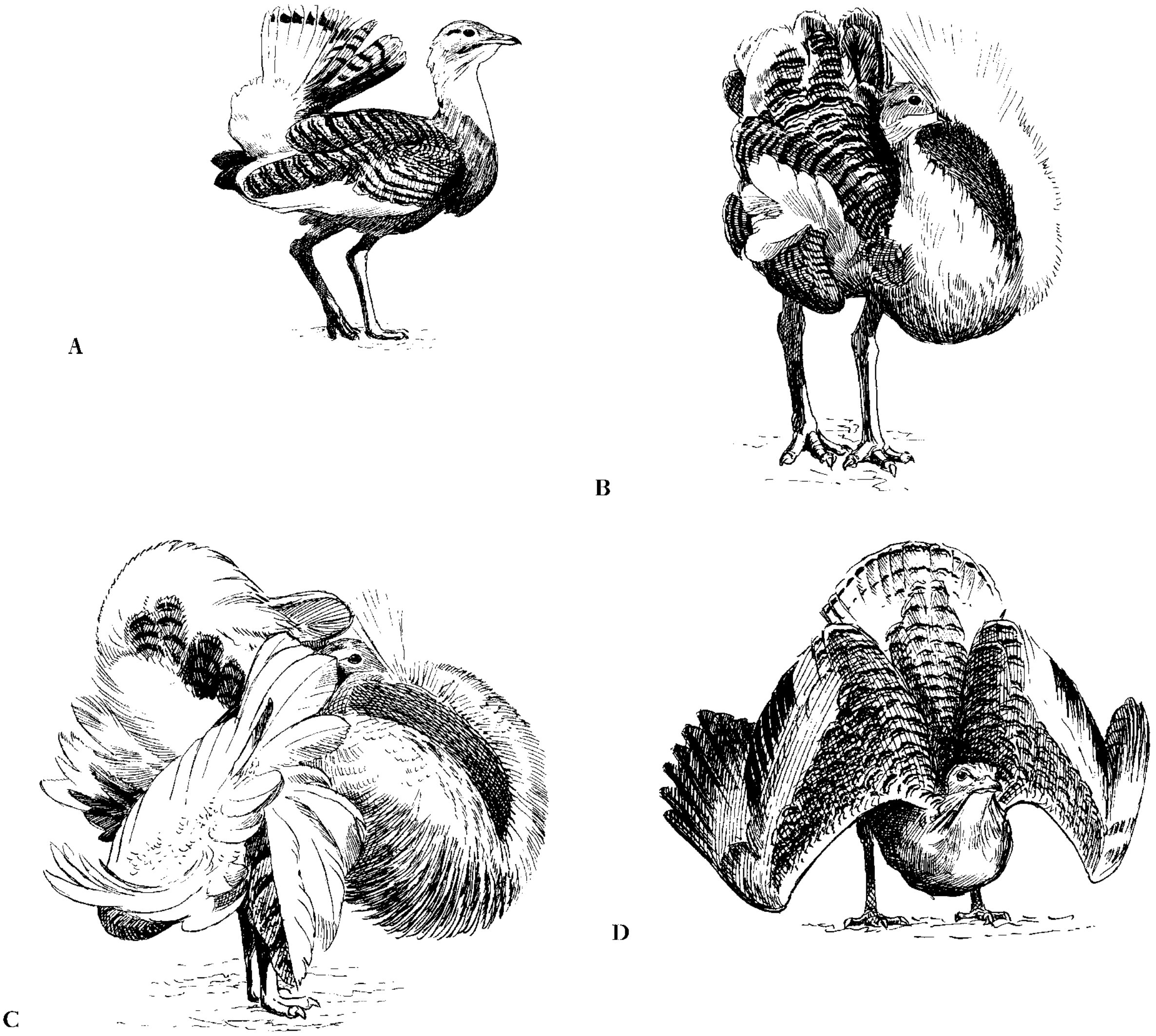

Fig. 3. *Otis tarda* Great Bustard showing breeeding behaviour: (A) charateristic springtime carriage of tail in sharp upright position, exposing elevated white under tail-coverts; (B) and (C) Balloon-display, and (D) Shock-display. Reprinted from *BWP* Vol. II, where part A after photograph by N J Collar, parts B and C after photograph by W Gewalt, and part D after Siewert 1939.

tail-coverts (Fig. 3A). Balloon-display (Fig. 3B and C) involves remarkable contortion which transforms (in matter of seconds) predominantly brown bird into almost entirely white one: gular pouch inflated by short series of gulps and exhalations into large pendulous balloon, exposing the two blue-grey stripes of bare skin down neck, and forcing head down and back into shoulders, thus causing whiskers (moustaches) on chin to point vertically upwards in front of eyes. Whole body steeply tilted tail-up, tail itself being cocked flat on back, almost touching head, and wings stretched down and back from shoulders (primaries still in folded-wing position) so that carpal joints trail near ground—in side view, forming perpendicular to forward-tilting body—while large white inner secondaries and lesser and median coverts twist forward and fan out. In this posture, male begins to trample with feet and, from time to time, wheels laterally, causing inflated gular pouch to swing about. Posture held for 10–15 s on average (Nečas and Hanzl 1956), but in south-western Spain average for full display time in April is 70 s (Hidalgo de Trucios and Carranza 1990) and 2 min average in Portugal (*BWP* Vol. II, p. 663), where longest full display up to 8 min and longest Display-posture held (including pauses when head raised for observation) up to 48 min. Display sometimes repeated at intervals of *c.* 1 min or longer, bird often walking short distance to new site, sometimes with gular pouch still partially inflated. Display rate and duration positively correlated with body size, age, and development of neck plumage and moustaches (Morales 1999). Relatively little exists of the competitive aggression among males associated with more crowded display-grounds of certain grouse (Tetraonidae). Males will wander past each others stations and even exchange places without conflict, though at safe distance; close proximity of females, however, apparently factor in generating inter-male hostility, and male displaying to female much more likely to treat another male as intruder than if displaying alone. Females come to display-ground individually, in twos, or in small groups; evidently attracted by conspicuous displays of males which may intensify when females sighted. Males individually approached by interested females; displaying birds often cautiously circled and watched. Though female may cause male to retreat at beginning of season, he more typically follows and attempts to circle her. Copulation may then occur; especially on periphery of display area. Mating success positively correlated with body size, age, and development of neck plumage and moustaches, as well as with rate and duration of display (Morales 1999).

Agonistic Behaviour. Excited half-grown and immature birds sometimes perform individual crane-like pirouettes, leaps, and bows; often thus induce others to behave similarly, especially in spring. Droves of subadult males, and sometimes older males, engage in sudden runs and rapidly intensifying chases, whole group finally running at full speed over area seldom more than 2500 m^2, executing precisely synchronized changes of direction (Gewalt 1959). Also show ritualized Plucking-dance (significance obscure): (1) run with jerks of neck and body in confused bunch; (2) one detaches himself, stands still, and assumes incomplete Balloon-display posture, often only raising shoulder feathers while producing protracted hissing and grumbling notes, trampling vehemently, and sometimes jumping; (3) other males form ring and run in circle round him; (4) after 10–30 s, stop, move in, and pluck feathers from back of motionless bird in middle with rapid jabs of bill (Gewalt 1959). Complete sequence of events does not always occur, sometimes only some of them. More frequent in early spring than later in the season (J C Alonso, C A Martín, and M Morales). Being largely non-territorial, aggression much reduced by social rank-order. Persistent springtime disputes between immature males (which may end as free-for-all involving many birds) may help establish such ranking. True fights recorded only in breeding season among mature males; usually of short duration, though may last up to 1 h (Gewalt 1959; J C Alonso *et al.*). May involve bill-sparring but birds mostly grip each other on neck, then shove and jostle; if one does not quickly flee, fight may more rarely end in submission, victor forcing losers head down until latter able to shake free (*BWP* Vol. II, pp. 664–5). Fighting generally preceded by long period of breast-to-breast confrontation in semi-display (one such lasted 110 min, ensuing fight 2.5 hrs): involves drooping of wings from shoulder (primaries remaining in folded-wing position), raising of shoulder feathers and wing-coverts, cocking and regular forward-fanning posture of tail, and bristling of under tail-coverts—with exposure of much white plumage; one or both may snap mandibles slowly and rhythmically, grunting occasionally and gently trampling (*BWP* Vol. II, pp. 664–5). Most intense threat display towards conspecific rivals and, in captivity, men and dogs, similar to that of cranes (Gruidae): head lowered until bird completely flat on ground with neck outstretched; if signal not respected, aggressor leaps violently to attack (Gewalt 1959). Females also show certain ranking tendencies, most obviously in harems of territorial males. Dominant female droops and raises folded wings from shoulder, adopting rolling gait with tail high in forward-fanning posture; pecks and chases other females, particularly those receiving attention from male, and brief tussles occur very rarely (*BWP* Vol. II, pp. 664–5). Females aggressive towards any male near nest. When startled by smaller terrestrial animal or low-flying bird, reacts with Shock-display (Fig. 3D): starting back, ducks low and brings up tail into fully fanned position, flashing wings open (carpal joints down, primaries up). Females with young will advance to attack such enemies, and wounded males tend to stay and fight rather than attempt to flee. Passing enemies usually avoided by squatting flat; men, however, cause birds to take flight, often at great distances (Gewalt 1959). Females on nest usually attempt to avoid intruders by squatting on eggs until almost trodden on, when flush off suddenly in great alarm (often deserting); rare individual females will, however, repeatedly crawl on belly from nest to safer distance and squat till danger past (*BWP* Vol. II, pp. 664–5).

Heterosexual Behaviour. See also Display-ground Behaviour. Female ready to mate stands close to male and watches his Balloon-display, sometimes initiating mating ritual by pecking at male's white feathers, particularly those around cloaca. Successful copulations involve progressively intensifying display by male as he follows and circles female over period of minutes. Female usually shows some alarm at vehemence of male's display, often twisting and dodging away, sometimes squatting only to rise again, sometimes running off completely. Male frequently flaps trailing inverted carpal joint down on female's back to induce her to squat; when female flat on ground, male stands over her—bringing wings out of full display position and partly deflating gular pouch—and then plucks repeatedly at her head for a minute or more until she rises beneath him and insemination occurs. Couple then instantly spring apart, body-shake, and usually self-preen; soon separate. Dominant female in harem (whether temporary or seasonal) much more rarely directs aggressive sexual displays to male, driving him away from other females with carpal joints drooped from shoulder in posture not dissimilar to that of male about to fight.

Relations within Family Group. For unilateral role of female in care of young, see Bonds and Breeding. Chicks may call from eggs up to 36 h before hatching, particularly intensely during emergence (Glutz von Blotzheim *et al.* 1973). Incapable of following female immediately after hatching, but may crawl into vegetation over rim of scrape when intruder near (*BWP* Vol. II, p. 665). May be led by female up to 100 m from nest within 24 h, showing well-developed following response; will also at times remain in vicinity of nest 3–4 days and be brooded in scrape (Dementiev and Gladkov 1951, England 1966). Though precocial, initially given single food items in bill by female at times; female also utters Food-call to direct attention to food resource. Young squat in response to calls of female when danger threatens. In heterosexual two-chick families, male chicks fed at higher rates than females, and remain closer to adult female (Martín 1997). Captive-reared male aged 18 days attempted to adopt Display-posture in response to human whistling (*BWP* Vol. II, p. 665; see also Voice).

Voice. (Updates *BWP* Vol. II, pp. 665–6)

Calls of Young. Downy chicks and fledglings have wide vocabulary, including following (*BWP* Vol. II, p. 666; Arance de Prada and Otero 1987). (1) Principal call. Penetrating, plaintive, high whistle ‘cheeeoo cheeeoo’ in descending glissando; first heard from egg before and during chipping. Acts as brooding summons to female; after hatching, also used as relocation distress call (Lost-call) when separated from female, developing into protracted whistling or wailing by weeks 4–5. (2) Calls of well-being. Trilling ‘prrrip’, rising in pitch; brief in downy chicks, slower and more varied in older young. Apparently develops into extremely muted, brief, pleasant siren note produced by contraction in chest causing cavity at base of neck to fill out, recalling faint klaxon of multi-tone car-horn; signifies well-being and may be heard from birds up to at least 2 years old. (3) Greeting-call. A short, powerful trill—‘trrip’—of level pitch; used when relocated by mother and given in response to her call (latter itself not yet adequately described). In captive birds, uttered in response to human whistling; in males, may be accompanied by attempted adoption of display-posture. As birds get older, becomes throatier and entirely vowel-less. (4) Call seeming to express alertness without alarm. A brief, musical ‘chewyoo’, given standing still. (5) Alarm-call. A short shriek; variable. Sometimes also uttered when small chick attempts to cope with hopping orthopteran prey. (6) Call used in defensive attack. A shrill, metallic ‘heng’. (Adult-like nasal bark given from third week of life.)

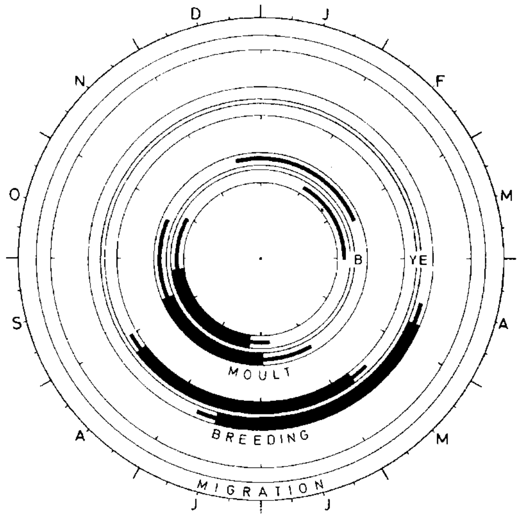

Fig. 4. *Otis tarda* Great Bustard breeding cycle. Reprinted from *BWP* Vol. II.

Breeding. (Updates *BWP* Vol. II, p. 666)

Season. See Fig. 4 for central Europe. Apparently similar throughout range.

Nest-site. On ground in low grass or crop; rarely in taller vegetation. In southern Portugal preferred cereal crops, followed by first-year fallows, older fallows, and plough land (Morgado and Moreira 2000). Nest: shallow depression, unlined except for few strands of vegetation sometimes (perhaps accidentally) trampled down to form sparse matting. Average diameter: 25–35 cm, depth 5–10 cm, sometimes less. Building: by female.

Eggs. Elliptical, smooth, and fairly glossy; variable in colour—pale grey, olive, olive-brown, olive-green, or (rarely) pale blue, well blotched light or dark brown. 80 × 57 mm (69–90 × 52–61), $n = 120$ (Schönwetter 1967). Weight 146 g (111–172), $n = 9$ (Gewalt 1959). Clutch: 2–3, rarely 1–4. In sample of 858 nests found in Hungary in 1974–90, average clutch size 1.93 (Faragó 1992), whereas in Portugal, average clutch size was 2.6 for $n = 16$, with modal value of 3 (Morgado and Moreira 2000). In former, no significant difference in clutch size found between early (April–May) and late (June–July) nests. One brood. Replacements after egg loss recorded in central Europe but thought less likely in Iberia (Gewalt 1959, England 1966), though at least one found in central Spain (J C Alonso, CAM). Laying interval 1–2 days.

Incubation. By female only. May be variable in length, as reported 21–28 days. Begins with first, second, or last egg; hatching usually asynchronous.

Young. Precocial and nidifugous. Cared for and fed by female. Fed bill-to-bill at first but gradually become self-feeding.

Fledging to Maturity. Fledging period 30–35 days. Become independent during first winter—especially males—though females tend to remain with mother up to beginning of following mating season; in rare cases young remain with mother for more than 1 year (Martín 1997, Alonso *et al.* 1998). Age of first breeding 2–4 years for female, 5–6 years for male.

Breeding Success. In long-term study in north-west Spain (Morales *et al.* 2002*a*), mean yearly population productivity was low (0.14 chicks/year, $n = 11$), as well as in sample of 32 marked females over same period (0.15 chicks/year). Inter-annual variability in population breeding success was high (0.04–0.29). Productivity was positively correlated with precipitation in winter (October–March) prior to each breeding season, as determinant of food abundance, and negatively with number of days of rain during hatching period (Morales *et al.* 2002*a*). Years of high annual productivity yielded higher proportion of females rearing two chicks. Individual breeding success higher in females older than 6 years compared with younger birds. Females breeding successfully one year normally fail the following, and females with higher than average individual breeding success tended to breed both in years of low and high population productivity, whereas those with lower than average bred successfully only in years of high productivity (Morales *et al.* 2002*a*).

Survival. (New section)

In north-west Spain, survival of chicks between the first and fourth months of life was only 30–40%, as estimated both from censuses and marked birds (Martín 1997). In central Spain, survival between 1 month and 1 year of age was *c.* 30%. However, total survival from hatching to 1 year probably much lower (*c.* 10–20%) (Martín 2001; J C Alonso *et al.*). Adult annual survival estimated *c.* 90% (Lane and Alonso 2001; J C Alonso *et al.*). After Gewalt (1959), maximum age *c.* 30 years in captive-reared bird. However, oldest free-living marked individuals of known age from north-west Spain, *c.* 15 years (E Martín).

Plumages. (Updates *BWP* Vol. II, pp. 666–7)

Subsequent Plumages. Following non-breeding plumages like adult, but breeding plumages only gradually acquire full adult characteristics. Younger females have more uniform grey neck and chest; older females have feathers here longer and narrower, pale yellow on foreneck, cinnamon on hindneck; in some, chest partially suffused cinnamon, purer ash-grey median coverts and outer tertials; in some, short moustaches. In males, intensity of cinnamon on chest and neck and length and density of moustaches increase with age (Carranza and Hidalgo de Trucios 1993, Morales 1999). Between *c.* third and sixth year, neck mainly grey with relative greater extension of cinnamon collar than older males, but with less intensity; later on as described under adult breeding. In old males, neck bright cinnamon, grading to vinous-chestnut on chest, and to creamy white on foreneck; long and dense moustache at each side of chin connected by shorter hair-like feathers on centre of chin.

Bare Parts. Moults. See *BWP* Vol. II, p. 667.

Measurements. (Replaces *BWP* Vol. II, p. 668) All are given in millimetres.

Netherlands, November–March; skins (Rijksmuseum van Natuurlijke Historie, Zoölogische Museum, Amsterdam). Bill to feathering above nostrils.

	sex	mean	se	no.	range
wing (adult)	♂	617	12.3	10	598–633
wing (juvenile)		560	18.3	5	540–582
tail (adult)		243	12.5	9	222–259
bill		36.8	2.07	14	32–40
tarsus		158	6.73	15	145–168
toe		71.6	3.42	14	65–78
wing (adult)	♀	486	7.25	14	475–497
wing (juvenile)		468	9.36	5	455–480
tail (adult)		214	4.01	13	208–219
bill		30.8	2.10	19	27–36
tarsus		125	4.39	19	118–132
toe		57.5	1.62	19	54–63

Sex differences significant. Juvenile wing significantly shorter than adult, but bill, tarsus, and toe similar and combined above. Juvenile tail *c.* 20 shorter than adult, first winter *c.* 5 shorter. Slightly larger wings reported by Glutz von Blotzheim *et al.* (1973) and by Dementiev and Gladkov (1951) probably because measurements made with tape along outer edge of wing rather than with wing flattened and stretched against ruler as in table above. In sample of 12 wild adult males measured *in vivo* in north-west Spain, wing length (tape along outer edge) 627.5 (600–655), tarsus length 157 (146–167), and moustaches 228 (200–260) (J C Alonso *et al.*). In sample of wild, 20- to 70-day-old chicks (92 males and 73 females) from north-west and central Spain measured *in vivo*, male wing length 451 (295–550), female wing length 382 (275–460), male tarsus length 126 (92–150), female tarsus length 108 (86–135) (Martín *et al.* 2000).

Weights. (Replaces *BWP* Vol. II, p. 668) All are given in grams.

(1) Adult, October–March; East Germany, south Russia, Italy, and Hungary combined (Heinroth and Heinroth 1927–8, Niethammer 1942, Dornbusch 1965, Moltoni 1968, 1969, 1971, Glutz von Blotzheim *et al.* 1973). (2) Adult, April–May; mainly East Germany (Glutz von Blotzheim *et al.* 1973), 1 south Urals (Dementiev and Gladkov 1951). (3) Summer, USSR and East Germany (Dementiev and Gladkov 1951, Gewalt 1959, Dolgushin 1962). (4) Juvenile, October–March; East Germany and Italy (Dornbusch 1965, Moltoni 1968, 1971, Glutz von Blotzheim *et al.* 1973). (5) Adult males, February–March; north-west Spain (J C Alonso *et al.*). (6) Chicks, July–August; north-west and central Spain (Martín *et al.* 2000).

	SEX	MEAN	NO.	RANGE	SEX	MEAN	NO.	RANGE
(1)	♂	883	11	5750–16000	♀	4421	11	3260–5250
(2)		11975	13	8500–18000		3816	4	3480–4025
(3)		–	–	7200–12200		3650	2	3400–3900
(4)		4506	5	4100–4908				
(5)		10500	12	8000–13000				
(6)		2494	92	1250–2700		1562	73	950–2300

In adult males, old birds usually heavier (younger *c.* 6000–12 000, older 8000–16 000); reported extreme of males of 21 000 or more not confirmed. Juvenile male in captivity reached 8150 mid-February (Heinroth and Heinroth 1927–8), but free living one 7000 in February (Morales 1999), juvenile female 4350 by December (Gewalt 1959).

Structure. See *BWP* Vol. II, p. 668.

Geographical variation. (Replaces *BWP* Vol. II, p. 668)

Slight. Eastern populations of nominated *tarda* tend to slightly paler upperparts with narrower black bars and more extensive grey on upperwing, but much overlap in colour with western populations. Recent studies reveal that, in Europe, western (Iberian) and central-eastern populations are genetically divergent, showing significant differences in distribution of 11 mitochondrial haplotypes and suggesting separation over *c.* 200 000 years, and perhaps different colonization paths, one for Iberian and another for central-eastern populations (Pitra *et al.* 2000).

Adults of east Asiatic *dybowskii* like adults of nominate *tarda*, but head and neck slightly paler grey, black bars on upperparts broader, more distinctly defined; all median and lesser upper wing-coverts, except those along forewing, grey with variable white tips; greater number of outer tail-feathers white; moustaches on each side of chin in adult male breeding connected by short bristle-like feathers on central chin. Differences between adult females of both subspecies less pronounced than between males; juveniles indistinguishable (Hartert 1921–2, Dementiev and Gladkov 1951).

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References

Alonso, J C and Alonso, J A (1990) Parámetros demográficos, selección de hábitat y distribución de la avutarda en tres regiones españolas. Colección técnica. ICONA, Madrid. *Ibis* **129**, 212–24.

Alonso, J C and Alonso, J A (1996) The Great Bustard (*Otis tarda*) in Spain: present status, recent trends and an evaluation of earlier censuses. *Biological Conservation* **77**, 79–86.

Alonso, J C and Alonso, J A (1999) Colisión de aves con líneas de transporte de energía eléctrica en España. In Ferrer, M and Jans, G F E (eds), *Aves y líneas eléctricas. Colisión, electrocución y nidificación*, pp. 61–88. Editorial Quercus, Madrid.

Alonso, J C, Alonso, J A, and Muñoz-Pulido, R (1994) Mitigation of bird collisions with transmission lines through groundwire marking. *Biological Conservation* **67**, 129–34.

Alonso, J C, Alonso, J A, Martín, E, and Morales, M B (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.

Alonso, J C, Alonso, J A, Morales, M B, and Martín, E (1996) Seasonal and interannual population dynamics of the Great Bustard (*Otis tarda*) at Villafáfila Reserve, NW Spain. In Férnandez Gutiérrez, J and Sanz-Zuasti, J (eds), *Conservación de las aves esteparias y su hábitat*, pp. 191–200. Junta de Castilla y León, Valladolid.

Alonso, J C, Alonso, J A, Martín, E, and Morales, M B (1998) Proximate and ultimate causes of natal dispersal in the Great Bustard. *Behavioral Ecology* **9**, 243–52.

Alonso, J C, Lane, S J, Dawson, R, and Idaghdour, Y (2000a) Great bustard *Otis tarda* in Morocco: status in spring 1999 and evudence of a decline in recent decades. *Oryx* **43**, 141–6.

Alonso, J C, Morales, M B, and Alonso, J A (2000b) Partial migration, lek fidelity and nesting area fidelity in female great bustards *Otis tarda*. *The Condor* **102**, 127–36.

Alonso, J A, Martín, C A, Alonso, J C, Morales, M B, and Lane, S J (2001) Long distance seasonal movements of male Great Bustards (*Otis tarda*) in central Spain. *Journal of Field Ornithology* **72**, 504–8.

Alonso J C, Palacín, C, and Martín, C A (2002) Status and recent trends of the great bustard (*Otis tarda*) population in the Iberian peninsula. *Biology and Conservation*, in press.

Andryushchenko, Y A, Arsievich, N G, Martynets, M M, Stadnichenko, I S, and Oleinik, D S (2000) Results of winter census of Great Bustard in the South of Ukraine, 1998–1999. *The Bustards in Russia and Adjacent Countries*. Moscow.

Antonchikov, A N (1998) The state of the Great Bustard population in Europe countries. The number of birds and influencing causes. In *Natural and Historical Memorials of Saratov Oblast*. Saratov.

Antonchikov, A N (2000) Great Bustard. In Stattersfield, A J and Capper, D R (eds), *Threatened Birds of the World*. Lynx Edicions/BirdLife International, Barcelona/Cambridge.

Arance de Prada, G and Otero, C (1987) El vocabulario en los pollos de avutarda (*Otis tarda*). In *I Congreso Internacional de Aves Esteparias*, pp. 21–4. Junta de Castilla y León, León.

Atta, G A M (1992) First record of great bustard *Otis tarda* in Egypt. *Sandgrouse* **14**, 111–2.

Bauer, W, Helversen, O V, Hodge, J, and Martens, J (1969) *Catalogus Faunae Graeciae*. Thessaloniki.

BirdLife International (2000) *Threatened Birds of the World*. Lynx Edicions/BirdLife International, Barcelona/Cambridge.

British Ornithologists' Union (1971) *The Status of Birds of Britain and Ireland*. Blackwell, Oxford.

Cabrera, M, Hernández, F, Ballarín, I, Pela, O E, and Guiral, J J (1987) Últimos datos sobre la distribución y el estado de la población de avutarda (*Otis tarda*) en Aragón. In *I Congreso Internacional de Aves Esteparias*, pp. 11–7. Junta de Castilla y León, León.

Carranza, J and Hidalgo de Trucios, S J (1993) Condition-dependence and sex traits in the male great bustard. *Ethology* **94**, 187–200.

Carranza, J, Hidalgo de Trucios, S J, and Ena, V (1989) Mating system in the Great Bustard: a comparative study. *Bird Study* **36**, 192–8.

Collar, N J (1985) The world status of Great Bustard. *Bustard Studies* **2**, 1–120.

De la Peña, J (1980) The great bustard (*Otis tarda*) in Spain. In *Symposium Papers on the Great Bustard* Otis tarda *and the Houbara Bustard* Chamydotis undulata. FISG/CIC/Game Conservancy, Athens.

Dementiev, G P and Gladkov, N A (1951) *Ptitsy Sovietskogo Soyuza I.* Soviet Science State Publishers, Moscow.

Dolgushin, I A (1962) *Ptitsy Kazakhstana II.* Izdat. Akad. Nauk Kazakhskoy SSR, Alma-Ata.

Dornbusch, M (1965) Zum Gewicht der Grosstrappe. *Falke* **12**, 104.

Dornbusch, M (1982) Population and conservation of Great Bustard (*Otis tarda*) in East Germany. In *International Symposium on the Conservation of Bustards in Western Europe and North-west Africa*. León.

Dornbusch, M (1987) Zur Dispersion der Großtrappe (*Otis tarda*). *Ber Vogelwarte Hiddensee* **8**, 49–59.

Eken, G and Magnin, G (2000) *A Preliminary Biodiversity Atlas of the Konya Basin, Central Turkey*. Türkiye Dogal Hayati Koruma Dernegi, Istanbul.

Elósegui, J (1985) *Navarra, Atlas de aves nidificantes*. Caja de Ahorros de Navarra, Pamplona.

Ena, V, Martínez, A, and Thomas, D H (1987) Breeding success of the Great Bustard *Otis tarda* in Zamora Province, Spain, in 1984. *Ibis* **129**, 364–70.

England, F (1966) Great Bustards in Portugal. *British Birds* **59**, 22–7.

ETI (1998) *Censo Regional de Avutarda en Castilla y León*. Dirección General del Medio Natural, Servicio de Vida Silvestre Consejería de Medio Ambiente y Ordenación del Territorio. Unpublished report. Junta de Castilla y León, Valladolid.

Faragó, S (1990) The effect of heavy winters on Bustard (*Otis tarda* L.) populations in Hungary. *Àllattanni Közlemènyek* **76**, 51–62.

Faragó, S (1992) Clutch size of the Great Bustard (*Otis tarda*) in Hungary. *Aquila* **99**, 69–84.

Faragó, S (1993) Development of Great Bustard populations in Hungary in the period 1981–1990. *Folia Zoologica* **42**, 221–36.

Faragó, S (1996) Lage des Großtrappenbesttandes in

Ungarn und Ursachen für den Bestandsrückgang. *Naturschutz Landschaftspflege in Brandenburg* **5**, 12–7.

Ferguson-Lees, I J (1959) Studies of less familiar birds 141. Great Bustard. *British Birds* **59**, 491–3.

Ferianc, O (1963) Rozšírenie dropa velkého *Otis tarda* L. na Slovensku (Verbreitung der Grossen Trappe (*Otis tarda* L.) in der Slowakei). *Biologia* **18**, 900–15.

Flint, V E and Mishchencko, A L (1991) The Great Bustard in the USSR. In Goriup, P D, Batten, L A, and Norton, J A (eds), *Status and Conservation of Lowland and Dry Grassland Birds in Europe*, pp. 89–90. Joint Nature Conservation Committee, Reading.

Fodor, T (1973–4) A Túzokpopulációk Letszámvaltozása Magyarszágon. *Aquila* **80**, 121–38.

Fodor, T (1977) *Nemzetközi Tüzokvédelmi Szimpósium Elöadásai, Sarkadramete 1976*, 45–9.

Fodor, T, Nagy, L, and Sterbetz, I (1971) *A. Túzok.* Mezôgazdasági Kiadó, Budapest.

Garzón, J (1981) El censo de avutardas confirma la regresión de esta especie. *Quercus* **1**, 17–9.

Gewalt, W (1959) *Die Grosstrappe.* Neue Brehm Bucherei, Wittenberg-Lutherstadt.

Glutz, U N, Bauer, K M, and Bezzel, E (1973) *Handbuch der Vögel Mitteleuropas*, Vol. 5. Akademische Verlagsgesellschaft, Frankfurt am Main.

Hartert, E (1921–2) *Die Vögel der paläarktischenFauna*, Vol. 3. Friedlander and Sohn, Berlin.

Heinroth, O and Heinroth, M (1927–8) *Der Vögel Mitteleuropas*,Vol. 3. Bermühler, Berlin-Lichterfelde.

Hellmich, J (1991) *La Avutarda en Extremadura. Monografías Alytes* 2. Adenex, Mérida.

Hellmich, J (1994) The Great Bustard (*Otis t tarda* L.) in Extremadura, Spain: distribution, status and conservation. Workshop on Great Bustards. Tiszafüred, Hungary.

Helmich, J (1999) The great bustard *Otis tarda* L. in Morocco, 1998. Unpublished report to the International Foundation for Conservation and Development of Wildlife. Inezgane, Morocco.

Hernández, V, Ortuño, A, Sánchez, M A, Villalba, J, Sánchez, P A, López, J M, and Esteve, M A (1987) Estado Actual de algunas aves esteparias en la región de Murcia. In *I Congreso Internacional de Aves Esteparias*, pp. 459–68. Junta de Castilla y León, León.

Hidalgo de Trucios, S J (1990) World status of the Great Bustard (*Otis tarda*) with special attention to the Iberian Peninsula populations. *Miscelánea Zoologica* **14**, 167–80.

Hidalgo de Trucios, S J and Carranza, J (1990) *Ecología y comportamiento de la avutarda (*Otis tarda*).* Universidad de Extremadura, Cáceres.

Hidalgo de Trucios, S J and Carranza, J (1991) Timing, structure and functions of the courtship display in male Great Bustard. *Ornis Scandinavica* **22**, 360–6.

Höglund, J and Alatalo, R (1995) *Leks.* Princeton University Press, Princeton, NJ.

Hohkov, A N (1998) *Rare Animals of Stavropol Region.* Stavropol.

Hummel, D and Berndt, R (1971) Der Einflug der Großtrappe (*Otis tarda* L.) nach West-Europa in Winter 1969/70. *J. Orn.* **112**, 138–57.

Isakov, Y A (1974) Present distribution and population status of the Great Bustard *Otis tarda* Linnaeus. *Journal of the Bombay Natural History Society* **71**, 433–44.

Kirikov, S (1960) Les changements dans la distribution des oiseaux de la partie européenne de l'Union Soviétique aux XVII^e–XiX^e siècles. *Proceedings of the International Ornithology Congress* **12**, 404–21.

Kollar, H P (1996) Action Plan for the Great Bustard (*Otis tarda*) in Europe. In Heredia, B, Rose, L, and Painter, M (eds), *Globally Threatened Birds in Europe*, pp. 245–60. Council of Europe, Strasbourg.

Kollar, H P and Wurm, H (1996) Zur Bestandssituation der Großtrappe (*Otis t tarda* L. 1758) in Österreich. *Naturschutz Landschaftspflege in Brandenburg* **5**, 7–9.

Kumerloeve, H (1968) Recherches sur l'avifaune de la République Aarabe Syrienne essai d'un apercu. *Alauda* **36**, 1–26, 190–207.

Lane, S J and Alonso, J C (2001) Status and extinction probabilities of great bustard (*Otis tarda*) leks in Andalucía, southern Spain. *Biodiversity and Conservation* **10**, 893–910.

Lane, S J, Alonso, J C, Alonso, J A, and Naveso, M A (1999) Seasonal changes in diet and diet selection of great bustards in north-west Spain. *Journal of Zoology* **247**, 201–14.

Lane, S J, Alonso J C, and Martín, C A (2001) Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas unoccupied? *Journal of Applied Ecology* **38**, 193–203.

Lewis, R A (1985) Do blue grouse form leks? *Auk* **102**, 180–4.

Ligon, J D (1999) *The Evolution of Avian Breeding Systems.* Oxford University Press, Oxford.

Litzbarski, B and Litzbarski, H (1996) Einfluß von Habitatstruktur und Entomofauna auf die Kukenaufzucht bei der Großtrappe (*Otis tarda* L., 1758): *Naturschutz und Landschaftspflege in Brandenburg* **5**, 59–64.

Lukschanderl, L (1971) Zur Verbreitung und Ökologie der Großtrappe (*Otis tarda* L.) in Österreich. *J. Orn.* **112**, 70–93.

Lütkens, R and Dangel, M (1975) The situation of the Great Bustard (*Otis tarda* L.) in Austria. *ICBP Bulletin* **12**, 212–6.

Lütkens, R and Eder, F (1977) Uber das Schicksal von Randpopulationen der Großtrappe (*Otis tarda* L.) in Niederösterreich. *J. Orn.* **118**, 93–105.

Martín, C A (2001) Dispersión y estructura genética de la población de avutardas de la Comunidad de Madrid. Ph.D. thesis, Universidad Autónoma de Madrid, Madrid.

Martín, C A, Alonso, J C, Morales, M B, Martín, E, Lane, S J, and Alonso, J A (1999) Censo de avutardas de la Comunidad de Madrid 1998. *Anuario Ornitológico de Madrid* **3**, 46–53.

Martín, C A, Alonso, J C, Alonso, J A, Morales, M B, and Pitra, C (2000) An approach to sexing young Great Bustards *Otis tarda* using discriminant analysis and molecular techniques. *Bird Study* **47**, 147–53.

Martín, C A, Alonso, J C, Alonso, J A, Pitra, C, and Lieckfeldt, D (2002) Great bustard population structure in central Spain: concordant results from genetic analysis and dispersal study. *Proceedings of the Royal Society of London B* **269**, 119–25.

Martín, E (1997) Dispersión juvenil y cuidado maternal en la avutarda (*Otis tarda*). Ph.D. thesis, Universidad Autónoma de Madrid, Madrid.

Martín, E, Alonso, J A, Alonso, J C, and Morales M B (1996) Evaluation of captive breeding as a method to conserve threatened great bustard (*Otis tarda*) populations. In Férnandez Gutiérrez, J and Sanz-Zuasti, J (eds), *Conservación de las aves esteparias y su hábitat*, pp. 131–6. Junta de Castilla y León, Valladolid.

Martínez, C (2000) Daily activity patterns of great bustards *Otis tarda*. *Ardeola* **47**, 57–68.

Moltoni, E (1968) Notizie sull'Otarda (*Otis tarda* L.) in Italia. *Rivista Italiana di Ornitologia* **38**, 223–34.

Moltoni, E (1969) Altre notizie sull'Otarda (*Otis tarda* L.) in Italia. *Rivista Italiana di Ornitologia* **39**, 55–6.

Moltoni, E (1971) Ulteriori notizie sull'Otarda (*Otis tarda* L.) in Italia. *Rivista Italiana di Ornitologia* **41**, 128–30.

Moore, H J and Boswell, C (1956) Field observations on the birds of Iraq. *Iraq Natural History Museum Publication* **9**, 10.

Morales, M B (1999) Ecología reproductiva y movimientos estacionales en la avutarda (*Otis tarda*). Ph.D. thesis, Universidad Complutense de Madrid, Madrid.

Morales, M B, Alonso, J C, Martín, E, and Alonso, J A (1996) Mating system in the Great Bustard: a review of published work in light of recent radiotracking results. In Férnandez Gutiérrez, J and Sanz-Zuasti, J (eds), *Conservación de las aves esteparias y su hábitat*, pp. 287–92. Junta de Castilla y León, Valladolid.

Morales, M B, Alonso, J C, Alonso J A, and Martín, E (2000) Migration patterns in male great bustards *Otis tarda*. *The Auk* **117**, 493–8.

Morales, M B, Jiguet, F, and Arroyo, B (2001) Exploded leks: what bustards can teach us. *Ardeola* **48**, 85–98.

Morales, M B, Alonso, J C, and Alonso, J A (2002a) Productivity and female individual breeding success in a great bustard *Otis tarda* population. *Ibis* **194**, 293–300.

Morales, M B, Alonso, J C, Martín, C A, Martín, E, and Alonso, J A (2002b) Male sexual display and attractiveness in the great bustard *Otis tarda*: the role of body condition. *Journal of Ethology* (in press).

Morgado, R and Moreira, F (2000) Seasonal and population dynamics, nest site selection, sex-ratio and clutch size of the great bustard *Otis tarda* in two adjacent lekking areas. *Ardeola* **47**, 237–46.

Nečas, J and Hanzl, R (1956) Sborn. *Krasjsk. Múzea Trnave* **2**, 1–30.

Niethammer, G (1942) *Handbuch der Deutschen Vogelkunde*, Vol. 3. Leipzig.

Osborne, P E, Alonso, J C, and Bryant, R G (2001) Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology* **38**, 458–71.

Palacín, C, Campos, B, and Pinilla, J (1996) Demografía y uso del hábitat de la avutarda (*Otis tarda*) en Castilla-La Mancha. In Férnandez Gutiérrez, J and Sanz-Zuasti, J (eds), *Conservación de las aves esteparias y su hábitat*, pp. 183–90. Junta de Castilla y León, Valladolid.

Palacios, F, Garzón, J, and Castroviejo, J (1975) La alimentación de la Avutarda (*Otis tarda* L.) en España, especialmente en primavera. *Ardeola* **21**, 347–406.

Pitra, C, Lieckfeldt, D, and Alonso, J C (2000) Population subdivision in Europe's great bustard inferred from mitochondrial and nuclear DNA sequence variation. *Molecular Ecology* **9**, 1165–70.

Purroy, F J (1982) Simposio internacional sobre conservación de avutardas en Europa occidental. *Quercus* **7**, 13–6.

Randik, A (1978) Status, protection and maintenance of Great Bustard (*Otis tarda*) in Czechoslovakia and in Europe. *Cs Ochrana prírody* **18**, 19–37.

Rocha, P and Moreira, F (1999) Censo da Abetarda no Campo Branco no período Fevereiro 97–Março 99. In Beja, P, Catry, P, and Moreira, F (eds), *Actas do II Congresso de Ornitologia da Sociedade Portuguesa para o Estudo das Aves*, pp. 93–5. Sociedade Portuguesa para o Estudo das Aves, Lisboa.

Salomonsen, F (1963) *Oversigt over Danmarks Fugle*. Munksgard, Copenhagen.

Sánchez, A, del Arco, E, Barrutia, C, Martínez, L C, and Bielsa, J (1994) Censos de avutardas (*Otis tarda*) en Extremadura durante 1981–94. *Actas XII Jornadas Ornitológicas Españolas*. Sociedad Española de Ornitología, Madrid.

Schönwetter, M (1967) *Handbuch der Oologie 1*. Academischer Verlag, Berlin.

Siewert, H (1939) *Z. Jagdkde*. **1**, 5–36.

Sterbetz, I (1975) Trappen-Probleme in Ungarn. *Falke* **22**, 222–6.

Sterbetz, I (1977) A Túzok (*Otis tarda*) környezet Magyarországon. *Aquila* **84**, 81.

Sterbetz, I (1981) Comparative investigations into the reproductive behaviour of monogamous, polygamous and unmated Great Bustard populations in Southeastern Hungary. *Aquila* **87**, 31–47.

Tomialojc, L (1972) *Ptaki Polski Wykaz Gatunkowi rozmieszcenie*. Warsaw.

Trigo de Yarto, E (1971a) La avutarda en España. XVIII Triennial General Meeting of the International Council for Hunting. Unpublished report. Federación Española de Caza Madrid, Madrid.

Trigo de Yarto, E (1971b) La avutarda, esa bella desconocida. *Vida Silvestre* **1**, 11–8.

Tucker, G and Heath, M (1994) *Birds in Europe: Their Conservation Status*. BirdLife Conservation Series no. 3. BirdLife International, Cambridge.

Verner, W (1909) *My Life among the Wild Birds in Spain*. J Bale, Sons & Danielsson Ltd, London.

Watzke, H, Litzbarski, H, Oparina, O S, and Oparin M L (2001) Der Zug von Großtrappen *Otis tarda* aus der Region Saratov (Russland)—erste Ergebnisse der Satellitentelemetrie im Rahmen eines Schutzprojektes. *Vogelwelt* **122**, 89–94.

Yeatman, L J (1971) *Histoire des Oiseaux d'Europe*. Ed. Bordas-Découverte, Paris.