

-Œ Otididae Chlamydotis



Macqueen's Bustard

Chlamydotis macqueenii 🚯

VU Vulnerable Names (41) Monotypic

Mimi Kessler, John Burnside, Peter Pyle, Nigel Collar, and Guy M. Kirwan

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Revision Notes

Introduction

The Macqueen's Bustard, also known as the "Asian Houbara," is an elegant landbird native to arid sandy semi-desert and steppe regions from Egypt east of the Nile River, through the Sinai Peninsula, east across portions of the Levant and Arabian Peninsula to the northwestern Indian Subcontinent and Central Asia, reaching through the Gobi Desert and into the Ubsunur Lake Depression. It is a partial latitudinal migrant with a complex migratory pattern. The species is sedentary and locally nomadic in southwest Asia, whereas Central Asian populations are strongly migratory, leaving their breeding grounds in August–October and arriving September–November on the non-breeding grounds. Different subpopulations migrate along different routes, and juveniles migrate independently of adults.

An unobtrusive and cryptic species, the Macqueen's Bustard is rarely seen or heard except during the elaborate courtship displays of males. During its display, a male produces a staccato series of deep knocking notes after running either in a line or a circle with its neck retracted into an "S" shape, the plume-like feathers on its head and neck erected, resembling a fancy

ruff.

The species was considered to be relatively common in the late 1800s and early 1900s, especially as a non-breeding visitor. However, by the 1930s, its numbers had entered a decline, the magnitude of which increased over the remainder of the 1900s as a result of severe over-exploitation, leading to the near extirpation of the species in many parts of its range. The Macqueen's Bustard continues to face considerable threats from overhunting, principally by falconry, as well as poaching, habitat degradation, and disturbance from human activities, especially in its non-breeding range. The only major approach to stem this tide has been the establishment of captive-breeding projects, which have been viewed as a means to both facilitate hunting and compensate for the losses it incurs. However, there is concern that large-scale and annual releases of captive-bred birds produced via artificial insemination could be threatening the integrity of wild populations.

Assessing the status and biology of wild populations of this species is challenging due to its elusive behavior and typically remote and inhospitable habitats, as well as large releases of captive-bred birds, and unquantified levels of hunting. Much of the published knowledge regarding the species' biology is derived from birds raised in captivity, and may differ from that of wild populations. Currently considered Vulnerable under IUCN Red List criteria, it is possible that the species should be reclassified as Endangered given its current numbers and trends.

Identification

Field Identification

A medium-large, rather slim-necked bustard with generally pale sandy upperparts and a white neck adorned by a vertical black stripe. When displaying, the plume feathers on the neck and head are erected.





Lateral view. Frontal view.

Similar Species Summary

Unlikely to be mistaken for any other species.

Similar Species

The <u>Great Indian Bustard</u> (<u>Ardeotis nigriceps</u>) is only found in a relatively small area of northwest India and adjacent Pakistan. Aside from being much larger (males 100–122 cm versus 65–75 cm in Macqueen's Bustard), the Great Indian Bustard has an all pale gray neck, darker, plainer brown upperparts, and black flanks.

The <u>Arabian Bustard (Ardeotis arabs)</u> overlaps with Macqueen's Bustard only narrowly in the lowlands on the western side of the Arabian Peninsula (where both species are now very rare) (1); it is also larger with an all-gray neck and a black cap.

The <u>Little Bustard (*Tetrax tetrax*)</u> is considerably smaller, and both sexes exhibit a different neck and head pattern; also, this species prefers agricultural landscapes as opposed to desert ones.

Although it has never been recorded there, Macqueen's Bustard could conceivably be observed west of the Nile in Egypt, i.e., within the range of the formerly conspecific Houbara Bustard (*Chlamydotis undulata*). Although identification would be most straightforward for a displaying bird, Macqueen's Bustard can be differentiated by its black-tipped white crown feathers (versus the all-white crown of the Houbara Bustard), white-based black neck plumes (versus all black), and a pale blue-gray foreneck base and breast in mature males (versus peppered black and white in Houbara Bustard).

Plumages, Molts, and Structure

Plumages

The Macqueen's Bustard has ten full-length primaries (numbered distally, from innermost p1 to outermost p10), 16–17 secondaries (numbered proximally, from outermost s1 to innermost s12 or s13, and including four tertials, numbered distally, t1 to t4), and 20 rectrices (numbered distally on each side of the tail, from innermost r1 to outermost r10). Longest primaries are pp7/8, pp7-10 are notched on the inner web, and pp6-9 are emarginated on the outer web (2). Little or no geographic variation in appearance has been reported (see Systematics). The following molt and plumage descriptions are based on those of Cramp and Simmons (2), Johnsgard (3), and Collar (4), along with an examination of Macaulay Library images (caution that some of which may involve captive-bred individuals not showing typical molt and plumage patterns). See Molts for information on Humphrey-Parkes molt and plumage terminology used by Birds of the World. Macqueen's Bustard appears to have alternate plumages (see Molts) although ornamental plumes appear to be formative or basic feathers, as found in cranes and ardeids (cf. 5, 6). Sexes are similar in Juvenile Plumage, differ on average in Formative Plumage, and differ more extensively in Definitive Basic and Alternate Plumages (based primarily on the development of ornamental plumes); definitive appearance may most often be attained at the Second Basic Plumage in females and at the Third Basic Plumage in males.

Natal Down

Present at the natal site, primarily in April–August. Down is short, thick, somewhat woolly, and comprises a complex pattern of creamy white and golden brown with blackish-brown edges, likened to a carpet (see image below). The head and neck are covered by a mass of stripes, with a brown forehead patch, white above and below the eye, a large golden-brown patch on the foreneck, and a pale hindneck. Upperparts include a golden stripe and U-shaped whitish border on upper back, four radiating white patches on the mid back, and rest of back, along with the sides and wings, mottled. Underparts creamy white.

Juvenile (First Basic) Plumage

Present primarily in July–December, on breeding grounds and likely during southbound migration in most birds. Similar to definitive basic female, but with the ornamental plumes on the head and neck reduced or absent. Crown uniformly tan; rest of head and neck mostly grayish, the sides of neck with short black marks as opposed to ornamental frilled feathering. Juvenile outer primaries and rectrices are narrower and more pointed or tapered at the tips than basic feathers, and the pattern to the rectrices is less distinct (buff with dusky bars and broad buff to tawny tips). The white areas of the upperwing coverts also average slightly duller. Note also that the wings and tail of juveniles are shorter than in adults, within each sex (2; see Measurements).





Juvenile commenc

Natal Down.

Formative Plumage

Present primarily in November (when fresh) to April or September (when worn), depending on the presence of a First Prealternate Molt (see below). Plumage transitions based on suspended, protracted, and incomplete Preformative Molts over first year, with head and back feathers usually being replaced before migration, and flight feathers being replaced and ornamental plumes developing more noticeably through winter and early spring on winter grounds. **Female** and **Male** differ on average but sexing is complicated by individual variation in timing of molts and maturation rates; by spring, sexing is possible for most or all birds by the increased development of formative ornamental plumes in males compared to females.

Formative Plumage is similar to Definitive Basic Plumage, but upperparts average duller yellowish gray; formative occipital plumes reduced and blackish in male and reduced or absent (without blackish) in female. Formative neck plumes (frill) shorter in both sexes: the formative feathers in male approximately equivalent to length of basic feathers of female and those of formative females short, not much longer than in juvenile (although with variation based on timing within the molt cycle). Formative blue-gray pectoral plumes of the male shorter and duller than basic plumes, and those of females usually off-white with some coarse barring and fine buff and black vermiculations laterally. In autumn and early winter, at least, formative back feathers and scapulars contrast with worn juvenile upperwing secondary coverts (although beware basic coverts are paler than upperpart feathers in all plumages). Retained juvenile flight feathers following incomplete molts (that can commence on non-breeding grounds and complete on breeding grounds) are characterized by being contrastingly short, narrow, tapered or rounded at the tips, and abraded, the juvenile primaries brownish with some buff or off-white marks at their tips and the juvenile rectrices with faded buff tips.





Formative Male

Formative Female.

First Alternate Plumage

Present primarily in May–August. This plumage may or may not exist, depending on whether or not a First Prealternate Molt exists (see Molts). If so, in perhaps some but not all birds, it will resemble Formative Plumage but have a few scattered new feathers, most likely on the crown and back. It may also be possible that some birds can show more extensive replacement as described under Definitive Alternate Plumage, below. Aging and sexing criteria given for Formative Plumage continue to apply in alternate plumages.





Formative or First

Formative or First Alternate Male.

Second Basic and Alternate Plumages

Present primarily in November (when fresh) to September (when worn). Second Prebasic Molt can begin on the non-breeding grounds and is completed on the breeding grounds (see Molts), leading to a protracted transitional period. Following molt, Second Basic Plumage is similar to Definitive Basic and Alternate Plumages in each sex, but, in some birds, mainly males, the juvenile outer primary (p10, occasionally up to pp7–10; see Molts) and some secondaries in the center of the tract can be retained during the Second Prebasic Molt, allowing identification of Second Basic Plumage; other remiges are uniformly replaced and show molt clines as in older birds (see below). In these, basic inner primaries and middle secondaries contrast with juvenile outer primaries and adjacent secondaries, which are narrow, brown, and abraded. Many birds (primarily females) have replaced all primaries and secondaries by Second Basic Plumage and these cannot be reliably separated from Definitive Basic Plumage. Second basic ornamental plumes of males may average less extensive than in later basic plumages; however, some males may defer breeding maturity for up to six years (4) and it is possible that males may not develop extensive plumes until three years old or older. Some or most (but possibly not all) individuals might be expected to replace some body feathers during a Second Prealternate Molt and thus be in Second Alternate Plumage, as described for Definitive Alternate Plumage, below.





Second Basic.

Second Basic or Alternate Male.

Definitive Basic Plumage

Present primarily in November (when fresh) to April or September (when worn), depending whether or not a Second Prealternate Molt occurred (see Molts). Crown buff with a sometimeshidden central line of white erectile feathers, each with a shaggy black tip. Rest of head pale grayish buff or (nape) white, with a black line on the side of the neck composed of erectile filamentous plumes (referred to as a "frill"), which broaden at the sides of the neck (often meeting on the nape) and turn white (usually hidden) ventrally; on the sides of the neck, these feathers are black basally, white tipped black in their central part, and are longer and all white on the lower part of the neck. Rest of upperparts from nape to uppertail coverts pale sandy buff or rufous sandy, coarsely mottled, vermiculated, lined, and barred dark brown, gray, and black. The tail is buff basally with up to four bluish-gray bars, each one edged with black, and a white tip that can be speckled black. The pattern to the remiges, visible in flight, has the outer primaries (pp7–10) white with black tips, the inner primaries (pp1–6) and secondaries largely black with narrow white tips, and the upperwing carpal and secondary coverts buff proximally (most lesser coverts, some with black teardrop-shaped marks) grading to white distally (most greater coverts) but with a rufous wash on the outer greater coverts, and narrow black subterminal bands to the median and greater coverts forming indistinct wing bars. The upper breast is blue-gray, with ornamental black-and-white feathers extending on the sides from the neck frill and forming a bib of longer ornamental pectoral plumes on the lower breast. Rest of underparts cream to whitish. Underwing coverts and bases to the secondaries and primaries largely white from below (cf. ML133216561 ♠).

Sexing Macqueen's Bustard in the field can be difficult. Although males average 10% larger in almost all morphometric traits than females (see Measurements), their values overlap and the plumage does not always exhibit obvious dimorphism, especially during the non-breeding season (2, 3). The best means of sexing by plumage is by the extent of the ornamental plumes, although because these develop slowly over the winter and early spring, time of the year must be factored in. Generally, males show a broader black neck-band and longer basic occipital and pectoral plumes than females at a given time of the year. When fully grown, the occipital plumes of definitive basic males may be up to 100 mm, the neck plumes up to 190 mm, and the pectoral plumes up to 120 mm in length (and apparently longer based on examination of

Macaulay Library images), whereas these values in definitive basic females are up to 70 mm, 110, and 90 mm ($\underline{2}$). Behavioral differences related to territoriality and courtship can also be used for sexing (see Behavior).



Definitive Basic Female, possibly commencing Prealternate Molt.



Definitive Basic Fe

Definitive Basic Plumage is separated from Formative and Second Basic Plumages by uniformly basic upperwing coverts and flight feathers, without retained juvenile feathers (see Formative and Second Basic Plumages, above). The outer primaries can show an even molt cline from browner p6 to blacker p10 based on protracted molt, with the outer primaries also broader, more truncate at their tips, fresher, and blacker than retained juvenile feathers. Often there will be Staffelmauser patterns among pp6–10, with two or three sets of feathers (defined as a more worn feather distal to a fresher feather; 7) indicating older birds, in at least Third Basic Plumage for those with three sets of primaries; these are more likely in males and may be rare in females. In addition, basic rectrices are uniformly broad and square-tipped (see middle image under Second Basic Plumage, above), and show whiter tips. Finally, ornamental plumes average longer within each sex. Length values and quantity for Formative males may be similar to those of Definitive Basic females (above), while those of Formative females are short and can hardly project beyond normal feathering (2). The ornamental plumes of Second Basic birds likely average in between those of Formative and Definitive Basic Plumages (cf. 8 and 9 regarding ornamental plume development by age in Great Bustard (Otis tarda)), but specific details are needed for Macqueen's Bustard.



Definitive Basic Male. Definitive Basic Male.

Definitive Alternate Plumage

Present primarily in March–August. In both sexes, Definitive Alternate Plumage is similar to Definitive Basic Plumage except that some scattered head and body feathers are renewed during a limited Definitive Prealternate Molt; this likely occurs in all birds, although some may forego this molt (see Molts). Ornamental plumes have reached full development by these months.



Definitive Alternate Female.



Definitive Alternat

Molts

Molt and plumage terminology follows Humphrey and Parkes (10) as modified by Howell et al. (11). Under this nomenclature, terminology is based on evolution of molts along ancestral lineages of birds from ecdysis (molts) of reptiles (cf. 12), rather than on molts relative to current breeding seasons, locations, or time of the year, the latter generally referred to as "life-cycle" molt terminology (13). Prebasic molts often correspond to "post-breeding" or "post-nuptial"

molts, prealternate molts often correspond to "pre-breeding" molts, and preformative molts often correspond to "post-juvenile" molts; however, there is a lack of equivalency due to different bases of definition, especially among birds that migrate between hemispheres or that reside at tropical latitudes (cf. 14), as is generally the case with Macqueen's Bustard. The terms prejuvenile molt and juvenile plumage are preserved under Humphrey-Parkes terminology (considered synonyms of first prebasic molt and first basic plumage, respectively) and the former terms do correspond with those in life-cycle terminology.

The Macqueen's Bustard appears to exhibit either a Simple or a Complex Alternate Strategy (cf. 11, 15), including complete prebasic molts, an incomplete preformative molt, and a limited prealternate molt in at least the definitive cycle; study is needed on whether or not a first prealternate molt occurs and thus if this species exhibits the Complex (if occurring) or Simple (if not occurring) Alternate Strategy (2); see below. The following is based primarily on information in Cramp and Simmons (2) augmented by an examination of Macaulay Library images.

Prejuvenile (First Prebasic) Molt

Complete, primarily June–July, on or near natal territory. Details of juvenile plumage development are needed.

Preformative Molt

Often termed "post-juvenile molt" but in migratory species can also include the "first prebreeding molt," in whole or in part, using life-cycle terminology (cf. 14). Incomplete (possibly sometimes complete in females?), occurring primarily in August–March, commencing on or near breeding grounds in August–October and completed on non-breeding grounds in November–March (2). Body feathers and lesser and median coverts usually start to be replaced prior to southbound migration, followed by suspension, with resumption of body-feather molt and incomplete molt of flight feathers occurring on the non-breeding grounds. Formative ornamental plumes might begin growing on or near breeding grounds but do not become more obvious until continued development during November–March on the non-breeding grounds.

Primaries and corresponding primary coverts are replaced distally (p1 to p10), secondaries may be replaced convergently from both ends of the tract, and rectrices are generally replaced distally (r1 to r10) on each side of the tail, with some variation possible; this molt sequence is maintained through subsequent prebasic molts albeit often with incomplete replacement. Males may typically replace the inner 3–5 primaries and females the inner 3–9 primaries on the non-breeding grounds, but more variation can be expected based on variable fledging dates. Extent of replacement of rectrices needs study, but in other bustards often the inner 3–5 pairs of rectrices can be replaced and the outer 5–7 pairs retained, or in some birds all rectrices are replaced. Replacement of secondaries even less studied but probably some feathers in the center of the tract can be retained in some birds, especially males.

First, Second, and Definitive Prealternate Molts

Often considered part of "pre-breeding molt" under life-cycle terminology. Definitive Prealternate Molt may or may not occur in Macqueen's Bustard; however, examination of Macaulay Library images indicates that it may occur in at least some individuals (see images under Alternate Plumages). If so, occurs primarily in February–April on the non-breeding

grounds and can include scattered feathers on at least the head and back, although some molt on non-breeding grounds may represent a continuation of Definitive Prebasic Molt suspended during southbound migration; Definitive Prealternate Molts are marked by feathers replaced twice during the molt cycle and are expected in species such as bustards that are exposed to substantial solar radiation. Second Prealternate Molt is likely similar in timing and extent but may involve on average slightly fewer feathers. First Prealternate Molt may not occur in this species, most feather replacement on the non-breeding grounds representing a continuation of suspended Preformative Molt. Further study is needed.

Second Prebasic Molt

Often considered "first post-breeding molt" under life-cycle terminology. Interesting split molt of bustards within their first 15 months of life here considered an incomplete Preformative Molt concluding on non-breeding grounds, followed by Second Prebasic Molt commencing on or near breeding grounds. As such, Second Prebasic Molt appears to be incomplete to (usually?) complete and occurs primarily in June–January, with most feather replacement occurring on or near breeding grounds, but molt of primaries and primary coverts (and perhaps secondaries and rectrices) completed on non-breeding grounds in some birds. Second Prebasic Molt may commence earlier and be more extensive than Definitive Prebasic Molt of breeders due to lack of nesting and associated energy constraints in yearlings and two-year-old birds that defer breeding maturity (cf. 4) but more study is required. As with Definitive Prebasic Molt, ornamental plumes are basic and may not be fully grown until early spring. When incomplete, up to three juvenile outer primaries may be retained (most often just p10 but up to pp7–10 in males and perhaps some juvenile secondaries in the center of the tract can be retained. See see images under Second Basic Plumage.

Definitive Prebasic Molt

Often considered "adult post-breeding molt" under life-cycle terminology. Incomplete to complete, primarily in July–January, with most feather replacement occurring on or near breeding grounds but molt of primaries and primary coverts (and perhaps secondaries and rectrices) sometimes completed on non-breeding grounds. Some individuals may show different or prolonged molt timing. Basic ornamental plumes typically start to be replaced on the breeding grounds, grow slowly, do not become fully obvious until late fall or winter, and complete growth in early spring. Macaulay Library images of Macqueen's Bustard and other bustards flying in active primary molt are uncommon, indicating that they may remain largely sedentary during these periods (primarily July–September).







Female undergoin

Primary molt commences in June or July, on or near the breeding grounds, and may involve complete replacement, especially in females. Following incomplete molts (especially in males), the subsequent prebasic molt appears to commence where the previous molt terminated, resulting in complex Staffelmauser (stepwise) molting patterns, whereby each molt series commences at the termination point of the previous prebasic molt while often initiating new series (16, 7, 6). Replacement in these individuals can thus proceed in two or three waves through the primaries, resulting in two or three "sets" of feathers following completion (7), especially among the longer pp6–10 which take more time to grow. Staffelmauser appears to be a product of insufficient time to undergo a complete wing feather molt but has adaptive benefits in producing multiple small gaps in the wing during molt, which retains wing integrity and ability to fly and forage (17, 18). Staffelmauser-like patterns appear also to occur among secondaries in bustards, and definitive prebasic molt of rectrices may also occasionally be incomplete, but study is needed as inferring completeness is complicated by suspension of molts.

In Gruiformes (of which Otidiformes used to be considered a part), molt of primaries is proximal (19), unlike the distal replacement of bustards, perhaps helping to justify placement of Otidiformes in a separate order. However, molt of primaries in the Gruiform family Sarothruridae (flufftails) is divided into two series, pp1–5 and pp6–10 and it appears quite possible that similar separate series occur in Macqueen's Bustard and other bustards, based on their complex molt patterns and an examination of Macaulay Library images (see below). In this case, Staffelmauser may be further complicated and would be expected to occur more frequently among pp6–10 than among pp1–5 due to the larger outer than inner primaries, requiring more time for complete growth (cf. 20). More study is needed on the interesting molting patterns of bustards.



Female completing

Male undergoing Preformative Molt of Primaries.

Bare Parts

The following is based on previously cited literature (2, 3, 4) along with Harrison and Castell (21) and an examination of Macaulay Library images. Bare-part coloration of adults and juveniles is apparently similar, but differs in nestlings.

Bill

In juveniles and adults the relatively strong bill (rather compressed dorso-ventrally) is bluish gray or greenish gray to yellowish or horn at the base of the mandible with a darker to blackish maxilla. In hatchlings it is initially blackish to olive-gray, then becomes gray with a narrow black band on the maxilla adjacent to the white tip. By the juvenile stage the bill has reached adult-like coloration.

Iris and Facial Skin

In juveniles and adults the iris is pale sandy to sandy olive or pale yellow, occasionally pale brownish orange. In hatchlings it can be paler and grayish, quickly becoming yellow by the juvenile stage. The orbital skin is gray with a darker slate inner rim.

Tarsi and Toes

In juveniles and adults the legs and feet are olive-gray to plumbeous yellow or medium-bright yellow. They may become brighter during the pre-breeding and breeding periods than during the molting and non-breeding periods (study needed). The foot comprises three very short cushioned toes, but no hind toe (22). Claws are dark gray to black. In hatchlings the legs and feet can be gray to olive-gray but quickly to become yellow by the juvenile stage.





Adult. Adult.

Measurements

Linear Measurements

Overall Length. 65–75 cm (males), 55–66 cm (females) (23).

Wingspan. 135–170 cm (24).

Wing Length. Males 393-431 mm; females 357-377 mm (24).

Males are significantly larger than females in wing, tarsus, and head measurements (25). Among 448 individuals measured by Alonso et al. (25), mean wing chord was 360.0 mm (females)/405.8 mm (males); mean tarsus length 91.0 mm (females)/102.8 mm (males); mean head length 97.4 mm (females)/107.1 mm (males). Jarrett and Warren (23) published a workable discriminant analysis based on a sample of captive stock from Pakistan that could identify the sex >95% of the time using multiple morphometric variables, but noted that no single morphometric trait could be considered so reliable.

From approximately 130 individuals measured by Jarrett and Warren (23), mean linear measurements of adults were as follows, in mm, with means and sample sizes in parentheses:

Head Length. Males 97.2–110.4 (103.65, n = 79); females 89.2–100.1 (95.01, n = 50).

Bill Length. Males 33.3–49.5 (41.82, n = 79); females 32.4–44.1 (38.12, n = 50).

Tarsus Length. Males 88.7–106.8 (99.91, n = 79); females 80.0–95.7 (88.26, n = 50).

Middle Toe Length. Males 35.0–57.4 (47.58, n = 78); females 33.8–48.4 (45.51, n = 49).

Mass

Males significantly heavier than females ($\underline{25}$). Males ca. 1,500–2,400 g; females ca. 1,100–1,700 g (based on data from northwest India, Mongolia, and Russia; 26, 27, 2, 24). Combreau

and Saleh al Baidani (28) reported variation in mass across the range of this species, with those breeding in Yemen lightest (average 1,610 g males, 1,140 g females) and in the eastern Caspian heaviest (mean 2,026 g males, 1,345 g females). Those breeding in Mongolia, which undertake the longest-distance migrations, average 1,760 g (males) and 1,212 g (females). On the wintering grounds individuals may reach greater weights, e.g., Meinertzhagen (29) reported mass of ca. 3,175 g (male) and 2,500 g (female) on passage in Arabia.

Systematics

Systematics History

Otis macqueenii J. E. Gray, 1832, Illustrations of Indian Zoology, Volume 2, pl. 47.—Himalayas, foothills northwest India (cf. 30).

The holotype, an immature said to have been collected by "General Macqueen" (see Nomenclature), is held in the Natural History Museum, Tring (Old Vellum catalog 37.12a) (31).

Traditionally (e.g., 32, 33) this species was treated as conspecific with the Houbara Bustard (*Chlamydotis undulata*) of North Africa and the Canary Islands, but that the two species (as recognized here) form reciprocally monophyletic groups is now well recognized (34, 35, 36, 37, 38, 39), and they are thought to have diverged almost one million years ago (37, 39). Combining these molecular data with courtship (see 40, 4, 41) and plumage features (42), as well as differences in vocalizations (43, 42), the case was gradually made for their treatment as separate species (42, 44, 45, 46), although not without dissent and concern that the differences described "may well be functionally relatively trivial and would not prevent interbreeding" (47).

Adopting the Tobias et al. (48) system of scoring phenotypic characters to determine taxonomic rank (where a score of seven or more denotes a species), del Hoyo and Collar (49) itemized and scored these differences as follows (*Chlamydotis macqueenii* features listed first): "Black-tipped white *vs* all-white crown with white-based black *vs* all-black ornamental neck plumes ([score of] 3); pale blue-grey *vs* finely peppered black-and-white foreneck base and breast in mature male (2); position of crown feathers in display, falling forward over bill *vs* sweeping up and back (2); vocal differences in display (sequence ends in series of notes rather than one single note) (2)."

Geographic Variation

Phenotypic Variation

Some variation described in morphology; for example, birds from Arabia reportedly have shorter wings and wider and longer skulls than do birds in the Indian subcontinent (50). These may represent differences between resident and migratory forms of the species, as skull size and wing shape are under strong selection in migratory populations of birds (51, 52). One source described plumage of birds in Arabia as intermediate between *Chlamydotis macqueenii* and Houbara Bustard (*Chlamydotis undulata*), specifically on the breast and upperparts (53), however others have noted little variation in plumage among wild birds (28).

Differences in plumage between captive-bred lineages and wild birds reported anecdotally, with more variability and aberrations among captive-bred birds. A white, adult male with dark gray eyes and a few black feathers on the crown was captured in Saudi Arabia; and another white male hatched at a breeding center in Uzbekistan (54).

Genetic Variation

Using 17 microsatellite loci from samples of 108 individuals, Riou et al. (55) identified limited yet significant overall intraspecific differentiation, expressed principally between resident Arabian populations, especially Yemen, versus migratory Central Asian populations, but population structure within the latter group was virtually undetectable except subtle differentiation of western Kazakhstan birds relative to more eastern populations.

Subspecies

Monotypic.

Related Species

Pitra et al. (34) and Broders et al. (35) remain the only published bustard phylogenies, and although all *Chlamydotis* taxa were sampled, only mitochondrial cytochrome b sequences were obtained. Unsurprisingly, these data resolved *Chlamydotis macqueenii* as the sister species of its sole congeneric, Houbara Bustard (*Chlamydotis undulata*). Divergence times of the two species have been debated in the literature: Idaghdour et al. (36) suggested they split ca. 430,000 years ago, whereas Pitra et al. (37) calculated a much older divergence time of ca. 1 million years. The latter projection was validated by Korrida and Schweizer (39) who, using more powerful analysis and broader sampling, predicted that the two species diverged during a period of extreme aridity approximately 0.9 million years ago. *Chlamydotis* sits in a clade with *Otis*, with these two genera being sister to a clade containing the species of *Ardeotis* and *Eupodotis* (34, 35).

Hybridization

Molecular research indicates that the two houbara species diverged approximately one million years ago (39), and interbreeding in the wild has not been documented.

Captive breeding was initiated prior to the relatively recent recognition of the two houbaras as separate species. In this context, hybrid offspring have been successfully created at large scale through artificial insemination.

Nomenclature

Vernacular Names

Often called the "Asian Houbara" (<u>56</u>), with the <u>Houbara Bustard (*Chlamydotis undulata*)</u> then usually referred to as the "African Houbara" (<u>57</u>).

Names in other languages:

حباری شرقیة :Arabic

Azeri: Gözəl baladoydaq

Chinese: 波斑鸨

Hebrew: חוברה מדברית

Karakalpak: Джек

Kazakh: Жек дуадақ

Kyrgyz: Жорго тоодак

Mongolian: Жороо тоодог

Persian: هوبره

Russian: Джек, Дрофа-красотка

Tajik: Чек

Turkish: Asya Yakalı Toyu, Yakalı toy

Turkmen: Togdary

Urdu: Tiloor

Uzbek: Йўрға тувалоқ

Scientific Name

Somewhat unusually, but not uniquely, the personage of "Macqueen" appears to be rather obscure:

"The identity of Macqueen remains a mystery. In the 1940s, Sir Hugh Gladstone made extensive enquiries concerning Macqueen at the British Museum, the Royal Scottish Museum, the India Office and the Bombay Natural History Society. He also placed advertisements in national newspapers, and though he received several suggestions there was no Macqueen with any ornithological connection. Whoever he was, Macqueen must have had more than a passing interest to acquire, preserve and transport a large bustard skin from India to Britain." (58)

Subsequently, Jobling (59) identified two possible connections:

- (1) Major (General?) Thomas R. Macqueen (1792–1840) of the 45th Bengal Native Infantry (see also 60).
- (2) J. McQueen (as referred to by Kirby $[\underline{61}]$), a Scottish philanthropist with an interest in natural history, who apparently donated £300 to Andrew Smith's expedition in South Africa in 1834.

Both of these hypotheses, however, remain essentially unproven, although the spelling of the name, the clear association with India, and the information attached to the holotype all argue more persuasively in favor of the first of these two options.

Fossil History

The fossil record is rather sparse due to the relative lack of palaeornithological research within the known distribution; however, a single bone of *Chlamydotis macqueenii* was recently discovered at an Early Neolithic site in southeast Turkey, outside the species' currently understood range (62). In addition, bones ascribed to *Chlamydotis* have been identified at archaeological sites in the Kurdistan region of Iraq, Israel, southern Jordan, and Turkey (63, 64, 65, 66); see also Fossil History under Houbara Bustard (*Chlamydotis undulata*).

Distribution

Distribution

Resident populations formerly bred across the Middle East (from northeast Egypt, the Sinai Peninsula and the Negev Desert) (67, 68), through parts of the Arabian Peninsula, including parts of Oman and Yemen (69, 70) and as far north as the Aras River basin in the southwestern Caucasus (71), east across Iran to western Pakistan (Balochistan) (72, 22). Currently the distribution of resident populations is reduced in extent and density, and in many areas supplemented or replaced with captive-bred birds of primarily Balochistani breeding stock (see Management). Migrant populations breed from northwest Kazakhstan and northeast Iran eastwards to the the southern portion of Dorngovi Aimag, Mongolia (73). Also, the species is still found in suitable habitats in adjacent areas of China; in Dzhungaria, northern Gansu, and north Bayannur Prefecture of Nei Mongol (73). These populations winter in northwest India (Rajasthan and Gujarat) and Iran, as well as formerly across much of the Arabian Peninsula, but few birds now reach Iraq or eastern Arabia (27, 74, 75).

Extralimital Records

Anomalous observations of this species during the years 2018–2024 in Azerbaijan, Georgia, southwestern Russia, and Turkey were the outcome of an unpublished experiment undertaken by the Sheikh Khalifa Houbara Breeding Center in Kazakhstan. This involved the release of individual belonging to the eastern Kazakhstan genetic lineage (which naturally migrates west, then south, in autumn) into western Kazakhstan, where they exhibited their inherited migratory behavior. Such behavior is maladaptive in western Kazakhstan, where populations naturally migrate due south and avoid crossing the Caspian Sea (76, 77, unpublished data from Lesobre et al. 2024 conference presentation). Observations of these experimental birds should not be taken as records of natural behavior.

Historically, the species has been noted as a vagrant (July–April, mainly October–December) $(\underline{78}, \underline{2})$ to many European countries, west to France (December 1807, February 1883, and 1910) $(\underline{79})$, Belgium (three in 1840s, January 2003) $(\underline{80})$, the Netherlands, and England (at least in Lincolnshire, October 1847, and Suffolk, November–December 1962) (81).

Other European countries and territories with records (many of them old, reflecting the species' catastrophic decline, and some vague or perhaps involving Houbara Bustard (Chlamydotis undulata) include: Cyprus (last record November 1979) (82), Czech Republic (September 1889) (83), Denmark, Finland, Germany, Greece (June 1841) (84), Hungary, Italy, Latvia, Malta, Poland, Romania, perhaps Spain (no definite records of either this species or Chlamydotis undulata) (85), Sweden, Switzerland, and Ukraine (2, 24). It has also wandered north to Azerbaijan (86), Türkiye (87), and Lebanon (88).

Historical Changes to the Distribution

In the late 1800s and early 1900s, the Macqueen's Bustard was considered to be common, especially as a non-breeding visitor to southwest Asia ($\frac{70}{20}$), but by the 1930s, declines, mostly as a result of overhunting, became evident ($\frac{90}{20}$). Beginning in the 1900s, marked declines in the species' breeding range and populations were apparent; a trend that may still be ongoing (see Conservation Status and reviews by $\frac{91}{20}$, $\frac{92}{20}$, and $\frac{73}{20}$). The resident form of the species was almost totally extirpated from the Arabian Peninsula in the 1970s ($\frac{94}{20}$) and from much of Pakistan in the 1990s ($\frac{95}{20}$).

By the first decade of the 21st century, the resident breeding population on the Arabian Peninsula was limited to just a few pairs in two or three widely separated areas (Harrat al-Harrah Reserve, northernmost Saudi Arabia, Jiddat al-Harasis Reserve, in central Oman, and part of eastern Yemen), and was augmented annually with birds bred from largely Pakistani stock at two additional sites (Mahazat as-Sayd Reserve, in west-central Saudi Arabia, and in the western United Arab Emirates) (96, 70).

In addition to its loss as a breeder in Kuwait, even wintering birds seem no longer to occur there $(\underline{24}, \underline{97})$. Further north in Iraq, the species was already declining in the 1940s. In the 2010s, breeding was still regularly reported by hunters in the south and west of the country, though these populations were 'heavily hunted with falcons' (98)

The population in central and southern Syria, said to be still common in the 1940s (99), has been hunted to virtual extirpation (perhaps exacerbated by habitat loss and degradation), with rather few records since the 1970s (100, 101, 102, 103).

In neighboring Jordan, the last definite evidence of breeding (unsuccessful) was in the early 1960s, although the species may persist in a few remote areas. The majority of records since the 1970s evidently involve non-breeders ($\underline{104}$, $\underline{24}$), augmented by the intermittent release of captive-bred individuals of Pakistani stock over the last decade.

In the extreme west of the distribution, Macqueen's Bustard has almost certainly contracted eastwards in Egypt, where it formerly occurred east of the Nile Delta and south through the Eastern Desert, but the species is now probably confined to Sinai, and even here may have been extirpated (105, 106).

At the northernmost edge of the species' range in the Western Palearctic, in the lowlands of the Aras River basin in the southwestern Caucasus (Armenia-Azerbaijan), there has been no confirmation of breeding since 1917 and the population must surely be extirpated ($\underline{24}$, $\underline{107}$). The Macqueen's Bustard perhaps also bred in neighboring Türkiye until the late 1800s, but definite evidence of this is largely circumstantial and threadbare (87).

With respect to migratory populations of Macqueen's Bustard, irregular releases of captive-bred birds, sometimes in large numbers, have been undertaken in Kazakhstan and Uzbekistan, e.g., more than 30,000 individuals had been released by one network of centers by 2020 (108). Releases have also been conducted extralimitally or on the margin of the species' distribution (109), as in the Republic of Tuva, where only four cases of nesting had been

previously documented, all on the border of Mongolia ($\underline{110}$), and in the Republic of Kalmykia in which there have been only three records of the species, none of broods ($\underline{111}$).

Habitat

Habitat

The Macqueen's Bustard inhabits semi-deserts, deserts, and wormwood steppe at lower and middle latitudes. It is usually found in places that are either uninhabited or only thinly inhabited by humans (2). At any season of the year, both resident and migratory populations occur on open, more-or-less arid plains, including areas with either a clay, sandy, or gravel substrate, such as sabkhas and sand dunes (preferably stabilized by herbage or shrubs), and with scrubby halophytic or xerophytic vegetation up to 1–2 m tall, but the species is generally very scarce in truly rocky areas (24, 70, 28). For example, in the Harrat al-Harrah Reserve in northern Saudi Arabia, which is largely dominated by hard volcanic (basaltic) rocks, Macqueen's Bustard is confined largely to rough, shallow, sandy wadis and depressions (70). The species is often seen in areas of sparse vegetation and poor soils, including salt flats, but may be responsive to growth of annual vegetation induced by rainfall (24).





Bird in its habitat; Gujarat, India.

Bird in its habitat; I

Habitat in Breeding Range

A large-scale study on the breeding grounds in Uzbekistan found that numbers of males were greater in areas with lower mean shrub height, more gravel and flatter surfaces, but were unaffected by sheep density. The composition of the vegetation had a clear effect on male density, which was highest in vegetation dominated by *Salsola rigida*, still high in areas of *Salsola arbuscula* and *Astragalus*, but lower in *Artemisia*, and lowest in *Calligonum* (112, 113). Nevertheless, differing shrub assemblages in this region appear to facilitate similar productivity (114). Nesting success was also unrelated to landscape rugosity, shrub frequency, or livestock density (114).

In Arabia, resident populations breed up to ca. 1,000 m elevation and in areas where mean summer temperatures fall within the range $27-38^{\circ}$ C, although they regularly exceed 43° C and sometimes reach 50° C, with rainfall averaging just 100 mm per annum (115, 116, 70). Though Macqueen's Bustard may inhabit areas with higher ambient air temperature if there is suitable vegetation structure, breeding may be unsuccessful.



Bird in typical habitat: Qoraqalpogʻiston Respublikasi, Uzbekistan
© John Burnside Qoraqalpogʻiston Respublikasi, Uzbekistan | 07 Apr 2017
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Habitat in Nonbreeding Range

Birds wintering in the United Arab Emirates used a sandy, slightly undulating habitat with a high density of shrubs of more than 30 cm in diameter, of which the most important species were *Haloxylon*, *Zygophillum*, *Panicum*, and *Fagonia*; suitable habitat patches averaged about 40 km² (117, 118).

Movements and Migration

Movement

Sedentary and locally nomadic in southwest Asia, with irregular wandering reported, apparently in response to drought (28). Central Asian populations are strongly migratory, departing their breeding grounds in August–October and arriving September–November to their wintering grounds, from the Persian Gulf states to northwest India, with some previously occurring west to Sinai and occasionally even west of the Nile (105) and as far south as Socotra (70). An old record, in November 1920, near Port Sudan (in northeast Sudan, on the Red Sea coast) involved a vagrant/migrant *Chlamydotis macqueenii* (119, 120, 121) rather than a more local but still wandering Houbara Bustard (*Chlamydotis undulata*), which species might be resident in Sudan (92, but see 122). Juveniles migrate independently of adults. Winter abundance in given areas varies from year to year, apparently in response to rain-related condition of habitat. Birds return north in March–April, although males start to arrive in Uzbekistan as early as the end of February and commence displaying immediately (123).

Dispersal and Site Fidelity

Natal Philopatry and Dispersal

Dispersal of migrant Asian populations is better studied than resident populations, for which there is very little information. Migrants monitored via satellite tracking showed natal philopatry on a regional level, with 88% (7.8% standard error) of first-year birds returning to their natal area and a median dispersal distance of 25 km (range 4–76 km) from the natal nest to centroid of the first spring return. Other first-year juveniles moved nomadically during their first year, passed their first spring at distances of up to 356 km from natal site, but returned to their natal population from the second year (124).

Adult Fidelity to Breeding Site and Dispersal

Tracking studies have demonstrated that males of Macqueen's Bustard (n = 20) are very faithful between years to a small and exclusive territory around their display site ($\underline{125}$, $\underline{77}$). Females are typically faithful to their breeding population, but not a particular nest site, and in one study nested on average 13.3 km (SD = 21.8; range = 0.6–70.1 km) between the last nest of the previous year and the first nesting attempt of the following year ($\underline{113}$), but females have been noted to also nest > 200 km away, yet return to regular sites in subsequent attempts (77).

Fidelity to Overwintering Range

Satellite-tracked migrating Macqueen's Bustard in Central Asia show moderate wintering site fidelity at a regional level, but this behavior can vary considerably between individuals. The mean distance between winter sites of adults was 44.7 km (28.6-70.0 km, 95% CI, n = 50). However, some individuals showed a capacity to make large interannual changes, with a range of 0.9-755.4 km between years, achieved through short-stopping and/or use of multiple wintering sites in a single year (77, see also 28). Of three wild juveniles tracked between their first and second wintering sites, two showed regional scale fidelity (26.9 and 61.0 km), with one of these (a male) remaining faithful to the same non-breeding area over three subsequent winters (mean distance = 14.9 km, 6.7 SE). The third wild juvenile wintered first in southern Iran, then spent its second winter 964.6 km to the north in Turkmenistan.

Migration Overview

In southwest Asia, principally sedentary but nomadic, whilst Central Asian populations are obligate long-distance migrants, undertaking migration between the semi-deserts of Central Asia and their wintering grounds from the Arabian Peninsula to northwest India $(\underline{76})$. These differences have important conservation impacts and implications for the management of captive breeding, which must consider migratory population structure as well as natal and release site fidelity (124).



The wintering grounds include northwest India.

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Timing and Routes of Migration

The Macqueen's Bustard typically departs the breeding grounds during August–October and arrives on the non-breeding grounds in September–November, returning north in March–April. In Kazakhstan, the species typically arrives between early March and early May, and departs from late August to late November (but mainly during the period mid September to late October), sometimes initially dispersing northwards from the nesting grounds (126). In Pakistan the first autumn arrivals are in October, and birds begin to depart the east of the country in late February, with the last leaving Baluchistan by early April (22).

Satellite tracking of breeding birds across 5,000 km of Central Asia, from western Kazakhstan to the Gobi Desert in western China, has revealed that different subpopulations follow different migratory routes (76). On the western side of the Zagros Mountains, eastern Iraq hosted wintering birds breeding exclusively in the northeast Caspian and northeastern Iran. On the western and southern edges of the Hindu-Kush, an area of some 400,000 km² mainly in southwest Afghanistan and northern Pakistan hosted wintering bustards originating from central Kazakhstan. Finally, Chinese birds were found in two main zones in winter, one on the eastern edge of the Karakum Desert in Turkmenistan and the other in the western Thar Desert, Pakistan.

Birds typically circumvent but sometimes overfly high mountain ranges. Easternmost populations fly westwards, then southwards, to their wintering grounds, skirting the northern edge of the Himalayan massif. Macqueen's Bustard is capable of flying ca. 220 km per day, but frequent stopovers are required (127).

A comparison (124) using satellite telemetry of migratory behavior in wild and captive-bred birds nesting or released in Bukhara province, Uzbekistan, has found that the released individuals initiated autumn migration 20.6 days later on average and wintered 470.8 km closer to the breeding grounds, mainly in Turkmenistan, northern Iran and Afghanistan, than wild birds, which predominantly wintered in southern Iran and Pakistan (juveniles and adults moved similar distances).

Resident breeders caught in eastern and southern Arabia, in Oman and Yemen, did not exhibit

migratory movements, but occasionally made non-seasonal small-scale movements seldom exceeding 100 km (28).

Migratory Behavior

The Macqueen's Bustard migrates largely after sunset, with 59% of movement at night and 6% during twilight ($\frac{28}{2}$), which behavior contributes towards collisions with powerlines ($\frac{128}{2}$). Adults and juveniles apparently migrate independently ($\frac{76}{2}$). Though many stopovers on migration are used for less than one day, some stopovers may last for a week or more. During longer stopovers, the area used varies in size from 130–834 km² (129).

Control and Physiology of Migration

Experimental translocations indicate that migratory direction and distance are under a considerable degree of genetic control (77). As translocated birds return to their site of release, releases of Macqueen's Bustard for the purpose of reintroduction must consider the geographic origin of breeding stock or risk the introgression of maladaptive migratory tendencies into wild populations.

Burnside et al. $(\underline{130})$ found that Macqueen's Bustard (n = 48 individuals) uses local temperature as a cue for spring migration departure. The same authors found correlations between temperatures on the breeding and non-breeding grounds, suggesting that temperature is a reliable cue that informs departure decisions. They noted that this migratory cue plasticity is likely to prove critical in response to climate change. Wind was also correlated with autumn movements, particularly for heavier males. In spring, individuals were noted to "exploit favorable winds", but did not seemingly use these as a cue, sometimes even departing into headwinds.

Diet and Foraging

Diet and Foraging

Diet and foraging behavior have been described via studies of excrement and stomach contents in several range states, as summarized below. Observations on diet have also been made for birds in captivity (e.g., 131, 132, 133, 134).

Feeding

Food Capture and Consumption

Launay and Paillat (135) described in reasonable detail the methods adopted by the Macqueen's Bustard in foraging. Birds orient their body slightly downwards, with the neck bent backwards on itself and the bill pointed downwards. Birds move slowly but purposefully, pausing when they encounter food.

When the food source is plant material, the bird adopts what Launay and Paillat (135) described as "picking posture" with precise and deliberate movements of the neck resulting in the taking of one food item at a time. When catching and handling animal food, one of four

behaviors is exhibited: (1) "sticking behavior", observed when birds were taking ants; (2) "chasing behavior", exhibited across short distances, terminating in a springing movement of the body; (3) "flying prey catching behavior", shown when birds (rarely) attempt to catch flying insects, occasionally accompanied by unimpressive leaps into the air; and (4) "large prey handling posture", used for tackling prey items such as scorpions.

Most active in the early morning and late afternoon, and even at night during periods of full moon, with males tending to remain active longer both diurnally and nocturnally than females $(\underline{136}, \underline{70})$. In areas where disturbance is higher, and during the warmest times of year, nocturnal feeding is apparently the norm $(\underline{22})$. The species will range widely in search of food, and has been recorded roaming more than 59 km in the course of a single day in northern Saudi Arabia $(\underline{70})$.



0:00 / 0:25

Bird foraging.

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Diet

Major Food Items

Apparently variable and opportunistic all year, with no clearly discernible seasonal or geographical pattern. The diet of *Chlamydotis macqueenii* includes a wide range of vegetable matter (including fruits, seeds, shoots, leaves, and flowers) as well as animal matter (chiefly Orthoptera and Coleoptera), but the species is also somewhat opportunistic, and has been recorded taking small snakes (Colubridae) and lizards (Agamidae, Lacertidae) (26, 29, 78, 27, 2, 137, 135, 70).

It has been suggested that young are fed almost exclusively invertebrates, in one case many cockroaches (J. Aharoni in $\underline{2}$).

Vagrants in the British Isles have been reported taking green seeds, buds, and flowers of marsh ragwort (*Senecio aquaticus*), blades of winter wheat, leaves of mustard and pea, snails,

caterpillars of moths (Lepidoptera), ground beetles (Carabidae), and an earthworm (see 2).



0:00 / 0:43

Bird hunting and eating a grasshopper.

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Quantitative Analysis

Some work in Arabia, based on fecal samples from wild birds has suggested that invertebrates form the majority of the species' diet; all 161 samples analysed in United Arab Emirates contained some invertebrate remains, including a significant proportion of nocturnal Tenebrionid beetles (Coleoptera), as well as grasshoppers, locusts (Orthoptera), solifugids, scorpions (Arachnida), and insect larvae (138). In the United Arab Emirates, plant food primarily involved *Dipterygium glaucum* (Cyperaceae), whilst the grass *Capparis spinosa* was important in northern Saudi Arabia, and *Haloxylon salicornicum*, *Farsetia stylosa* leaves, and *Ziziphus* fruits were also taken (138).

Birds wintering in Iran regularly visit crops of alfalfa and salad rocket ($\underline{139}$), and in Pakistan the species is said to be strongly attracted to mustard ($Brassica\ campestris$) and $Eruca\ sativum$ crops, favoring succulent shoots, but will also take Orthopterans (mole crickets, grasshoppers) and beetles (Coleoptera), as well as berries of $Ziziphus\ nummularia$, flowers of $Capparis\ aphylla\ and\ C.\ decidua\ and\ succulent\ leaves\ of\ Haloxylon\ and\ Grewia\ populifolia\ (<math>\underline{140}$, $\underline{141}$, $\underline{142}$, $\underline{143}$, $\underline{22}$). An analysis of stomach contents (n=29) in the same country, involving birds hunted by falconers in early and late winter, found the early winter sample had fed predominantly on plant matter (74%), with most of the remainder comprising insect remains (25.3%) ($\underline{144}$). In contrast, animal matter comprised up to ca. 90% in some individuals in the late winter, including large quantities of dung beetles (Scarabidae) and tenebrionid beetles, and smaller numbers of ants ($Camponotus\ spp.$). Over both periods, plant material averaged 42.2% of the diet, with young shoots predominant in early winter, but seeds and flowers more

important in late winter, with the main species being *Anabasis* sp., *Tribulus terrestris*, *Haloxylon ammodendron*, and *Alhagi camelorum*, and much smaller quantities of *Artemisia*, *Salvia*, and *Atriplex*, all of which are strongly aromatic (144). Another study, also based on winter-hunted birds in Pakistan (*n* = 34), reported that plant material (78% by mass) comprised parts of seeds, leaves, flowers, and young shoots belonging to 19 plant species of 11 families, of which *Dipterygium glaucum* (91% of samples and 40% of total dry mass), *Capparis decidua* (65% and 2.7% respectively), *Haloxylon salicornicum* (35% and 1.7%), and *Farsetia hamiltonii* (32% and 11%) were the most important, whilst among animal matter the most frequent species were *Adesmia aenescens* (94% of samples and 11% of total dry mass), *Pimelia indica* (24% and 2.2% respectively), and *Arthrodosis* sp. (21% and 2.5%), with the proportion of animal matter appearing to increase between October and February (145).

In a 12-year study on the breeding grounds in Kazakhstan's Kyzylkum Desert, weekly studies of excrement and, to lesser extent, stomach contents, plants constituted the bulk of the diet through mid-May (146), with *Poa bulbosa*, *Bromus tectorum*, *Carex* spp., and leaves of *Oedibasis apiculata*, *Salsola* spp. and *Tulipa* spp. commonly taken. The percentage of plant content declines through the early summer, replaced by increasing percentages of invertebrates, particularly tenebrionids, solifugids and buprestids. By autumn, vegetation is lacking from the diet, the bulk of which comprises Isopods, Formicidae and to a lesser extent Blattodea through September. Mice, lizards, bees, and caterpillars were occasionally consumed by some individuals.



Bird feeding on insect.

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Food Selection and Storage

Information needed on food selection. Food storage not reported.

Nutrition and Energetics

Estimates of the energetic value of the prey suggested that on average this species must consume around 670 desert invertebrates/day to meet its energy needs, and the effort required to catch these prey may vary at least ten-fold seasonally (138).

Metabolism and Temperature Regulation

Captive-reared bustards (mass = 1,245 \pm 242 g, mean \pm S.D., n = 7) were estimated to have a resting metabolic rate of 261.4 kJ day⁻¹ in summer, and 23% higher in winter (147). Both

Macqueen's Bustard and its congener <u>Houbara Bustard (Chlamydotis undulata)</u> are well adapted to hot temperatures, living in summer environments where temperatures regularly exceed 40°C without becoming hyperthermic (<u>147</u>). Gular fluttering is observed, and birds adapt their foraging behavior in hotter months, seeking shade during the day under shrubs and foraging primarily at night as revealed via satellite tracking and field observations.

Drinking, Pellet-Casting, and Defecation

It is considered to be adapted to survive without drinking ($\underline{26}$). In Arabia, free-ranging individuals apparently do not drink, but rather obtain all of their liquid requirements from green plants and animal prey ($\underline{70}$), but in Pakistan, while not an obligatory or regular visitor to water sources, it appears that the species will drink occasionally ($\underline{140}$, $\underline{143}$). In Jordan, Mountfort ($\underline{148}$) observed up to 50 individuals visiting a pool to drink and, in Arabia, Meinertzhagen ($\underline{29}$) claimed that the species will descend wells for this purpose, which sounds curiously unlikely!

Sounds and Vocal Behavior

Sounds and Vocal Behavior

Very rarely audible and potentially largely silent. Mate selection and recognition principally undertaken using elaborate visual courtship display supplemented with a booming acoustic element.

Vocalizations

Development

Chicks have been noted to give a plaintive fluting call which becomes a penetrating hoarse piping note when frightened (J. Aharoni in 2), whilst small young will emit plaintive moaning sounds when handled (A. N. Poslawski in 2). In captivity, juveniles and subadults of both sexes are heard to utter weak and monotonous mewing notes in alarm or when restless (131); under similar circumstances, adults produce a low ventriloquial croaking note (H. Mendelssohn in 2, 24).

Vocal Array

The displaying male produces a staccato series of deep knocking notes emitted at a rate of 25–40 notes over 12-18 seconds ($\underline{149}$).

Adult females utter hissing notes when defending the nest or young (A. N. Poslawski in $\underline{2}$), and a female that had just returned to a nest with eggs gave an extremely soft *quop* or *quip* note, which was hardly audible more than 1 m away (P. A. D. Hollom in $\underline{2}$). Females produce a low-intensity grunt when presenting food to chicks (135).

Nonvocal Sounds

None reported.

Behavior

Behavior

Ethograms for Macqueen's Bustard were published by Mendelssohn et al. (150), Ponomavera (151), and Launay and Paillat (135), with Collins (152) listing similar behaviors for the closely related Houbara Bustard (*Chlamydotis undulata*). Borrowing from the other prior sources, Launay and Paillat (135) listed and extensively described a wide range of behaviors covering resting, grooming, feeding, social, and breeding.

Locomotion

Like many bustards, this species rarely flies from danger but prefers to walk or run away, though above all it relies on its cryptic coloration (and by squatting down) to escape predation. After running away, the bird may pause to relocate the threat, then run farther, fly a distance, and squat upon landing; alternatively, however, sometimes a fleeing bustard may take flight immediately, then run on after landing again (N. J. Collar in 2).

Flying is said to commence with a short take-off run, although perhaps not always (152), followed by extending the neck. As expected for such a large-bodied bird, the wing action is slow and on shallow wingbeats (a reasonably slow flick) (24). Flight as measured by telemetry is typically 50–60 km/h with exceptional flights of > 100 km/h probably achieved with the assistance of tailwinds (28). Approximately 35% of migratory flights are undertaken at an altitude of 100 m or less above ground level, and flights above 800 m above ground are rare (28). Distances flown by migratory bustards are considerable, as described under Movements and Migration. Migratory flights are primarily nocturnal (28).

Gait is similar to that of many other bustards, with a slow walk described as "mincing". In alarm the species will jerk its neck back and forth in a manner said to recall the movements of a swimming Eurasian Moorhen (*Gallinula chloropus*).



0:00 / 0:24

Bird running among vegetation.

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Self-Maintenance

Self-maintenance behaviors were illustrated and described in detail by Launay and Paillat (135). Preening is undertaken with a closed bill. The tail, breast, and neck feathers are most frequently groomed. Three positions of dust-bathing have been described: sitting; lying on the side; and crouching with neck pressed into the dust. Sunbathing is exhibited with either one or both wings extended and observed only when temperatures exceed 30°C (135).



A bird stretching.

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Agonistic Behavior

Physical fights between males have been reported anecdotally on the breeding grounds ($\underline{26}$). Threat posture, adopted against conspecifics or smaller terrestrial mammals, involves cocking

and fanning the tail, drawing the neck backwards to form a slight "S" shape, and half-opening the wings with the carpals pointed downwards; females will defend their nests in this position while emitting hissing calls (135, 2). Launay and Paillat (135) noted aggressive chasing by both sexes when foraging. A captive, half-fledged young was observed to squat low when a large raptor appeared overhead, but in response to a stranger would puff itself up and trail one wing, whilst the presence of a dog or cat would prompt the bird to stretch its neck high, bristle the crown and ruff feathers, half-raise the wings, call anxiously, and peck at the air (J. Aharoni in 2).



Female adopting threat posture against intruders.

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Sexual Behavior

Mating System

The male plays no part in parental care, and a brood may include chicks sired by several different males (125). In a breeding population in southwest Kazakhstan, males were faithful within and between years to a small and exclusive territory centered on their display site. Females nested near male territories and sometimes inside them, but did not favor the territory of their mate for nesting. This is inconsistent with a hypothesis of resource-based female choice, and implies that the breeding system of Macqueen's Bustard can be treated as a special case of lekking, albeit without male aggregation (125). It has been suggested (based on observations in Kazakhstan and Turkmenistan) that the mating system may be partially density dependent, with males displaying alone in areas of low density but groups of males gathering at traditional display grounds at relatively more densely populated sites (123); alternatively, such observations may have occurred outside the height of the breeding season.



0:00 / 1:31

Male displaying; April, Mangghystau oblysy, Kazakhstan.

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Courtship, Copulation, and Pair Bond

The display of the male commences with the neck held upright and the feathers at the base of the neck and on the head partially erected, accompanied by slow walking. This is followed by spontaneous and often quite prolonged periods of running (either in a straight line or in circles) while the neck is tucked in to form an "S" shape. During the latter phase, the neck feathers are fluffed up and held fully erect in such a way that they almost cover the head completely. Differences in display behavior (and appearance) from Houbara Bustard (Chlamydotis undulata) were elucidated in some detail by Collar and Combreau (41). In captivity, during days preceding egg-laying females are observed to perform similar displays, involving the raising of neck and crest feathers and running with mincing steps (28).



Male displaying.



A male in display.

Social and Interspecific Behavior

Solitary during the breeding season, but gregarious otherwise, tending to form same-sex flocks when sufficient conspecifics are present.

Predation

Red fox (*Vulpes vulpes*) is considered the most prolific mammalian predator of this species, taking eggs, chicks, and adults (28). In a three-year study of captive-bred and released chicks and juveniles in Saudi Arabia, 42 of 85 individuals were predated (153), with 75% of these losses due to mammalian carnivores, and the remainder attributed to raptors including Steppe Eagle (*Aquila nipalensis*) and Eurasian Eagle-Owl (*Bubo bubo*). An investigation of predated clutches (*n* = 58) in the Bukhara region of Uzbekistan identified desert monitor (*Varanus griseus*), foxes (*Vulpes* spp.) and hedgehogs (*Paraechinus hypomelas* or *Hemiechinus auritus*) as the most common predators (154). Smaller carnivores such as the steppe polecat (*Mustela eversmanii*), Rüppell's fox (*Vulpes rueppellii*), and Blanford's fox (*Vulpes cana*) represent threats to nests and chicks. Monitor lizards (*Varanus* spp.), rat snakes (*Elaphe* sp.), and ravens (*Corvus* spp.) have also been observed to predate bustard nests (155).

Breeding

Phenology

Residents. In the northern Arabian Peninsula, eggs are laid from February to May, with chicks seen as early as March (70). Similar in Oman, but with a second breeding season yielding chicks from October to November (70). Display commences in the Negev (Israel) in late December, with hatching between late March and mid May (106, 156, 68). Season March—May in Syria (106, 156). Nests have been found in the Harat steppe of Iran from mid-March to mid-May (157) and apparently March—April in Pakistan (158).

Migrants. Earliest displays observed in southern Kazakhstan in early April, with most nesting between mid-April and May (158). In Uzbekistan's Kyzylkum, earliest nests in the second half of March, with median nesting date in the first week of April (114). In southern Turkmenistan, nests are found in the first week of April, and in the southern Ustyurt in the second half of April (159). In northwest China, a three-year study found that the start of laying varies between 6 and 17 April, but the modal date fell consistently between 26 and 30 April (160).

Nest Site

The species nests on arid plains in semi-desert areas, sandy or stony sites, or in sparse scrub at desert edges. Based on a study in central Iran, the species selects breeding sites with a higher availability of insects and a higher vegetation density (*Artemisia sieberi* and *Seidlitzia rosmarinus* communities), but which are located far from relatively dense plant patches (157). In Central Asia, nests can be sited between 0.74 km (Uzbekistan) and 1.48 km (Kazakhstan) from the nearest displaying male (123), though a small sample of genetic parentage (n = 6) found no preference for females to nest within the territory of the father of her chicks (125). Vegetation around the nest in Kazakhstan typically comprises *Artemisia*, *Astragalus*, *Salsola*, *Carex*, *Ceratocephalus*, *Romaria*, and *Alium* (161).

In western China, nesting females clearly preferred areas with low-stature cover, and shunned densely covered and taller vegetation sites, whilst the number of herb species was significantly lower at nest sites than would have been predicted at random (162). Only the distance to the nearest fox (*Vulpes*) den contributed to discrimination between successful and predated nests, with the average distance to the closest fox den significantly greater at successful nests than at predated nests (162).



Female on its nest; general view.

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Nest

Construction Process

Site selected, visited twice before egg-laying and nest scrape prepared, by the female (2, 28).

Structure and Composition

A shallow and unlined scrape on ground, sometimes in open desert, but usually in the shade of some cover (2, 161, 24).

Dimensions

Scrapes are typically 130–220 mm in diameter ($\underline{2}$, $\underline{161}$, $\underline{24}$). Scrape can be 20–30 mm deep (156, 161).

Maintenance or Reuse of Nests

A female is generally understood to nest in the same general area every year, though the specific site of the nest will change by 100 m to 30 km (28).

Eggs

The eggs of this species have a relatively larger yolk and relatively less albumen than those of the <u>Houbara Bustard (Chlamydotis undulata)</u> (163). Note, however, that the samples used in this study were from captive lineages, for which deviations in egg weight and volume have been associated with age, inbreeding, and generations in captivity (164).

Shape

Short elliptical to short subelliptical (21).

Size

Mean 62.2×45.0 mm (21) or 62.3×45.1 mm (n = 140) (27). Size is noted to vary geographically, with smaller eggs in Yemeni populations and larger eggs from southern Iran through Central Asia (28).

Mass

Variously reported as 62.2-66.1 g (n = 3) ($\underline{161}$); 65-69 g (mean 67 g, n = 4) ($\underline{2}$); average 66.2 g but ranging from 45.7 to 104.0 g ($\underline{28}$).

Color and Surface Texture

Smooth and glossy, and color greenish olive to olive-brown, heavily and evenly marked with chocolate-brown longitudinal streaks and long blotches (2, 21).



Nest with two eggs.

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Clutch Size

Resident populations generally lay smaller clutches of 2–3 eggs, whereas migratory populations lay 3–5 eggs, with six eggs rare (22, 28). In western China, mean clutch size was 4.0 ± 0.8 (range 2–6) for early clutches and 3.3 ± 1.1 (range 2–5) for late clutches (160). In Uzbekistan, average clutch size is 3.2 ± 0.6 eggs (range 2–5) and clutch size declined between the first and second nesting attempts by 0.6 eggs (165, 166). In the Negev (Israel), barring a single-egg clutch that was probably incomplete, all other nests (n = 15) contained 2–4 eggs, mean 2.8 ± 0.7 (156). Eggs are usually laid at ca. 48-hour intervals (156, 28).

Number of Clutches

Single-brooded (2, 21), but the species will lay a replacement clutch within two weeks if the first is lost (2, 28). In Kazakhstan, these "second" clutches (2.7 ± 0.3) were on average smaller than initial clutches (3.3 ± 0.2) (155). Females in Uzbekistan had a 0.657 $(\pm 0.048$ SE) probability of renesting which was negatively related to date of nest failure, with third attempts being very rare (167).

Incubation

Incubation is by the female alone, including all night. Males with a brood patch have been reported in Russia (see $\underline{2}$), however no evidence of males having taken part in incubation has ever been found during extensive nest camera studies ($\underline{167}$, $\underline{154}$, $\underline{165}$). Incubation period usually 24 days, but occasionally up to 28 days ($\underline{2}$, $\underline{156}$, $\underline{21}$). Females begin incubation in earnest only after the clutch is complete ($\underline{28}$). Observations at a nest in Uzbekistan over a period of four days (before the eggs were predated) revealed that the female spent between 20.2% and 37.9% of each day off the nest, with each off-bout having a duration of between 21.2 and 39.3 minutes per day ($\underline{161}$). Females in China left the nest five times per day, for 8–26 minutes each time, moving a maximum of 1 km from the nest to feed ($\underline{28}$). Male may remain close to the nest, even when the young hatch, including at night, using 3–5 different roost sites within 50–60 m of the incubating female (A. N. Poslawski in 2).



Female incubating.

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Hatching

Observations in Israel indicate that hatching intervals within a single clutch are 2-24 hours, and females stay on the nest for a few more hours after all the chicks have hatched, until the down of the last chick is dry (156). In two cases, females continued to incubate eggs which failed to hatch for 24 hours after the last fertile egg had hatched, before deserting the nests concerned (156). Overall, both synchronous and asynchronous hatching has been recorded, indicating that incubation sometimes (but not always) commences with the first egg (2).

Young Birds

Described by Cramp and Simmons (2) and Harrison and Castell (21) as follows. Down is short, thick, and somewhat woolly, comprising a complex pattern of creamy white and golden brown with blackish-brown edges, likened to a carpet. The head and neck are covered by a mass of stripes, with a brown forehead patch, white above and below the eye, a large golden-brown patch on the foreneck, and a pale hindneck. Upperparts: a golden stripe and U-shaped whitish border on upper back, with four radiating white patches on the mid-back; rest of back, sides, and wings mottled. The underparts are creamy white.



Downy chick.

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Parental Care

The young are tended exclusively by the female, being brooded when small, and are provisioned directly by their mother for the first few weeks of life before they begin self-feeding (2, 21). Once young leave the nest, the brood and the adult female are rather mobile, especially by day (considerably less so at night) (161).



Female adopting threat posture to protect its chick.

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Cooperative Breeding

Unknown.

Brood Parasitism by Other Species

Unknown.

Fledgling Stage

Fledging period ca. 35 days (2, 21).

Immature Stage

Young stay with their female parent into their first autumn but migrate independently ($\underline{124}$). Family parties sometimes band together in autumn, and also join up with males ($\underline{2}$). Age of first breeding not known, but in captivity maturity is reached at two years old, perhaps earlier in females (H. Mendelssohn in $\underline{2}$).

Demography and Populations

Measures of Breeding Activity

In the Negev Desert (Israel), a study over four seasons of 16 nests containing 45 eggs found that 33% were lost due to predation, whilst 12% were unfertilized or contained dead embryos. The probability of an egg hatching was 0.34, and of a chick surviving to adult size 0.10. Under these conditions, a lifetime of 9.14 years would be required to maintain the population, with no growth (156).

In Uzbekistan, productivity has been found to be greater in areas with taller mean shrub height (range 13–67 cm) within 50 m of the nest; but clutch size (mean = 3.2 eggs) and per-egg hatchability in successful nests (87.5%) does not differ with laying date, shrub assemblage, or livestock density (114). In Kazakhstan, 12 nests and seven broods were found during a study in 1996, which suggested that nest failure due to predation was in the region of 17–22%, with a total of 8% of eggs being cracked (perhaps as a result of accidental damage caused by tortoises *Erionomys horsfieldi*), and brood size was routinely reduced to two young within the first two to three weeks after hatching (155).

Over three consecutive years (1998–2000), a total of 45 nests in Xinjiang province, northwest China, were monitored by Combreau et al. (160). They found that average nesting success over the three seasons was $0.588 (\pm 0.270)$, varying from -0.882 in 1998 to 0.530 in 1999 and 0.351 in 2000, with increased predation in the last two years, chiefly by Corsac fox (*Vulpes corsac*) and Long-legged Buzzard (*Buteo rufinus*). Overall hatchability, i.e. the proportion of eggs hatched in successful nests, was $0.839 (\pm 0.238)$, and mean brood size at hatching varied from $2.9 (\pm 0.8)$ to $3.3 (\pm 0.9)$ depending on year, with no significant decrease in brood size observed during the first five days post-hatching. In 1999 and 2000, brood size diminished sharply (14% and 27%, respectively) in pre-fledging chicks, whilst a further severe decrease (37%) was observed in 2000, probably due to raptor predation. Across the three-year study, a successful female would raise on average 2.3 ± 0.9 chicks to fledging and would lose $30.2 \pm 14.9\%$ of its broods, with the proportion of females that lost their entire broods being 0.181 in 1998, 0.708 in 1999, and 0.453 in 2000; only $55.3 \pm 26.3\%$ of females that successfully hatched eggs reared chicks to fledging, with overall chick production 0.827 per breeding female per year, and the probability of an egg producing a fledgling was 0.190 (160).

Life Span and Survivorship

Natural life span is not well understood for wild birds, and undoubtedly has been shortened considerably due to anthropogenic causes, especially hunting. In captivity, this species is known to reach ages greater than 20 years.

Disease and Body Parasites

Most observations of disease and parasites in this species have been reported from captive-breeding facilities, where these birds are held at higher density than encountered in the wild, and also may be exposed to diseases not present in wild populations (168, 169). Among viruses, Newcastle disease and avian pox were reported most commonly in a summary of clinical findings over 25 months in captive-breeding facilities in the United Arab Emirates (170). An outbreak of avian pox occurred in a flock of bustards received in Bahrain in February 1993; the birds displayed conjunctivitis, excessive lacrimation, and papilloma-like growths forming amorphous clusters on the third eyelid and on the conjunctiva (171). A captive group in Saudi Arabia was afflicted by chlamydiosis, resulting in some deaths and lesions in other individuals (172). Infections with *Staphylococcus*, *Pseudomonas*, *Mycoplasma*, *and Aspergillus* have also been reported at captive-breeding centers (170, 169). Paramyxovirus type 1, avian pox, chlamydophila, and trichomonosis are among the most common infectious diseases diagnosed in smuggled individuals of Macqueen's Bustard (173).

Helminth parasites are observed at relatively high rates in the feces and carcasses of free-living bustards (169).

Causes of Mortality

In China, nest predators included Corsac fox (*Vulpes corsac*) and <u>Long-legged Buzzard</u> (*Buteo rufinus*) (160). In Israel and Kazakhstan, <u>Brown-necked Raven</u> (*Corvus ruficollis*) has been implicated in nest losses (174, 156, 155). The monitor lizard *Varanus griseus* is also a predator of eggs (161).

Population Spatial Metrics

Calculations of density vary depending upon the season and methodology employed. During the breeding season on the Buzachi Peninsula of Kazakhstan, Combreau (175) found a marking-resighting method to give a density eight times higher (0.81 houbara per km²) than circular observations performed along a transect (0.11 houbara per km²), with the latter method biased towards the detection of displaying males.

During the breeding season males intensively use a small territory, $1.9-3.5 \text{ km}^2$ in size (75% kernels), which does not overlap with those of neighboring males (125).

Nests are usually separated by 5-10 km, but can be as close as 1-2 km apart (24).

Population Status

The most recent global estimate of the species' population is 33,000-67,000 mature individuals (176). A summary report to the Convention on Migratory Species in 2014 indicated a population of 74,030-86,340 individuals (177).

The resident population is currently distributed from the Arabian Peninsula to the Nag Valley in Baluchistan, Pakistan, and was estimated in 2014 to comprise 1,840–4,300 individuals (177). The most significant resident breeding population, and that least affected by large-scale

releases of captive-bred birds, is undoubtedly in Iran, and is estimated at 1,000–3,000 individuals (177). The resident (breeding) population in Pakistan was estimated at < 100 individuals in the late 1990s, but has likely been eliminated by hunting (178, 22, 92, 73). Fewer than 100 breeding pairs are estimated in the Arabian Peninsula and fewer than 30 in Iraq (179).

Among migratory breeding populations, the number breeding in Turkmenistan has declined to approximately 20 individuals (180). Numbers in Uzbekistan were estimated by Goriup (92) to comprise 2,200-2,700 breeding females and perhaps 6,000-9,000 individuals overall, concentrated across the western two-thirds of the country. More recently, surveys of 14,300 km² of the Kyzylkum Desert produced an estimated 1,645–2,030 breeding males (181) and perhaps 4,000 birds in all (182) including 2,350 breeding females (167), but numbers are declining. Nevertheless, the species also remains reasonably common in other areas with appropriate habitat in Uzbekistan (183). The breeding population in Kazakhstan was estimated at 30,000–40,000 individuals by Goriup (92) and ca. 49,000 in spring during 2006–2009 (184). Decades of fieldwork in southern Kazakhstan yielded a population estimate of 5,000– 6,000 individuals for that region (146), and in Mangystau a minimum of 6,500 individuals, and possibly as many as 13,000–19,000, in work published in 2004 (146). The species has only ever occurred marginally within Russia, with just four breeding records in Tuva (110), and a single sighting of a displaying male in Saratov and Kalmykia (111). Satellite tracking indicates breeding by some individuals in northern Afghanistan (177). In China the species was not discovered until the 1980s, and a 1994 survey over 14,900 km² of northern Xinjiang province produced an estimate of 280-525 individuals, from which Goriup (92) derived an overall national population estimate of > 500 birds. Thereafter, additional work upped the approximate numbers to 2,000 (160, 185) and subsequently to 6,000-8,000 individuals (186, 177). Mongolia holds perhaps 200–300 individuals (187).

This species is observed during winter in northwest India and westwards. Currently, few migrants occur as far west as the east coast of the Arabian Peninsula. The status of Macqueen's Bustard in Afghanistan is poorly known, but recent work using satellite telemetry suggests that large numbers migrate through the country's western plains (188, 76, 55) and thus may also overwinter in the country. Periodic censuses of the wintering population in Iran, conducted at approximately 370 sites in 16 provinces, found slightly fewer than 4,000 individuals in 2018, a 10% decline versus the previous year (189, 190). Numbers wintering in the Indian subcontinent have been estimated as follows. Totals wintering in Baluchistan, in western Pakistan, calculated to comprise 20,000–25,000 in the 1980s (191) and 19,000 in the 1990s (92), with some 4,854–6,268 in Punjab in 1999 (192) and 4,746–6,085 there in 2001 (193). Allinson (93) thought that the overall population in Pakistan in winter might number 23,000–27,000 birds. Confounding contemporary population estimates in Pakitstan are restocking efforts, which have released tens of thousands of captive-bred individuals primarily in Cholistan and Punjab, but also in Sindh and Balochistan (at least 20,000 captive-bred birds imported from the UAE from 2017–2023, alone; https://houbarafund.gov.ae/breeding-release) and the activities of hunting parties (see Effects of Human Activity: Hunting). In northwest India, Goriup (92) conjectured that 2,000–5,000 individuals might occur in winter, whereas Allinson (93) speculated that 3,000–3,500 could be present at this season, but Collar et al. (73) considered that the evidence for either estimate is weak.

Population Regulation

Hunting, both legal and illegal, represents the most substantial limitation on population growth or persistence (73). As described under <u>Predation</u>, a variety of mammalian, avian and reptile predators feed upon nests and chicks, and to a lesser degree, adults.

Conservation and Management

Conservation Status VU Vulnerable

VULNERABLE. CITES Appendix I and CMS Appendix II. The species is listed globally as Vulnerable (A4a,c,d) by BirdLife International, according to IUCN Red List Criteria version 3.1 (176) because of an ongoing rate of decline exceeding 30% (but less than 50%) over the past three generations, with an estimated population of 33,000–67,000 individuals. Status everywhere difficult to gauge owing to the species' highly cryptic coloration, elusive behavior, and generally remote and inhospitable habitat, but the overall population is believed to number fewer than 100,000 individuals and it is possible that the IUCN category Endangered could be more appropriate (73).

Resident Breeding Populations

A regional assessment of the species in the Arabian Peninsula evaluates Macqueen's Bustard as Critically Endangered (A2, A3, A4a,b,d and "probably" C1 with very "rapid declines") (179). In the first years of the 21st century the total wild and reintroduced breeding population of this species in Arabia was thought to number no more than 200 breeding females, most of them in rather remote protected areas, of which there were ca. 100 in Oman, perhaps 30 in northern Saudi Arabia, and 20 in eastern Yemen, and approximately 50 reintroduced birds (70). As of 2023 no wild resident populations persist in Saudi Arabia, although a population reintroduced into Mahazat as-Sayd Protected Area and reinforced over a period of 30 years with annual releases of captive-bred individuals of largely Pakistani stock, now numbers approximately 100 individuals. Despite that the number of released pairs in the Al Marmoom Desert Reserve (United Arab Emirates) was estimated at 50–300 individuals, it was noted that many of these are probably not wild per IUCN guidelines, despite released birds having bred successfully since 2007 (194). Consequently, the breeding population of wild resident Macqueen's Bustard in the United Arab Emirates was estimated at < 50, and the species is listed as Critically Endangered in the national Red List of the United Arab Emirates (195). The reasonably well-protected population in the Negev (Israel) has fluctuated in response to hunting pressure, but since the cessation of such activities in the 1970s the total number was in the region of 400–600 birds, but by the 1980s only ca. 100 pairs, being limited by habitat loss (to agriculture) and grazing pressure (106, 156, 196, 68, 24). The population was evaluated as Endangered nationally in 2017, with a decrease of 1.5% annually over the past two decades (197). This represents an uplisting from the Israel national status of Vulnerable in 2002. In Iran, the species is treated as Vulnerable, as the country uses the international evaluation of the species to guide its management. The species no longer breeds in nations of the Caucasus, although there were a few breeding records near the Arys River historically (198).

Migratory Breeding Populations

In Turkmenistan, Houbara is listed as Endangered (C2a(i)) (199). In Uzbekistan, as Vulnerable

(D) (200). In Mongolia, as Vulnerable (A2b,c,d+3b,c,d) (201). In China, Endangered (A2c,d+3c,d; C1) (202). Within Kazakhstan, the species is listed as Category II ("Catastrophically declining") (203), with declines of 50% estimated between 1998 and 2002 (204). Similarly steep declines were thought to have occurred in Kazakhstan between 2000 and 2009 (184) whilst demographic modeling in Uzbekistan indicates an ongoing decline of 9% per year (167).

In more marginal areas of the species range: in Tajikistan the species is listed as Critically Endangered, and in Kyrgyzstan as Category III, Critically Endangered (R, A1) ($\underline{205}$). Macqueen's Bustard is listed as Status I (Critically Endangered) in Russia, with the number of individuals in the northwest Caspian assessed at just 20 ($\underline{206}$, $\underline{207}$). As this area lies within the geographic extent of the Regional Assessment for Europe, the status in Europe is considered Critically Endangered/Possibly Extinct (Criterion D) ($\underline{56}$).

On the wintering grounds in the Indian subcontinent, Macqueen's Bustard is listed on Schedule I of India's Wildlife Protection Act (208), which provides the highest level of protection. In Pakistan, the species is listed on Schedule III, which also affords the highest level of protection.

Trends

Populations are in decline across the entire range of the species, primarily due to overhunting. Other threats include intensive agricultural practices, human disturbance, local persecution, and habitat degradation. Powerlines are also a cause of mortality likely to increase in importance as renewable energy infrastructure expands across the range of this species (182, 73, 128, 209).

Captive-breeding centers for both resident and migratory forms of Macqueen's Bustard provide substitute quarry for falconers and for restocking. However, mortality rates of released birds appear to be too high to mitigate and compensate for the loss of wild adults to hunting (210), and there are concerns regarding the genetic swamping of small remnant wild populations with maladaptive genes resulting from generations of production in captivity via artificial insemination.

Effects of Human Activity

Habitat Loss and Degradation

Although not the principal causal factor in this species' decline, livestock grazing in the breeding areas may locally remove desert vegetation at a scale capable of causing declines (91, 43, 211, 212, 213). Grassland habitats on the wintering grounds in northwest India have been degraded by plantations of *Prosopis juliflora* and its subsequent invasive spread (73). Extensive mining and oil exploration activities may be causes of habitat degradation in western China (73). Though grazing in breeding areas has been associated with low nesting success in Israel (106, 156), research in the Kyzylkum Desert, Uzbekistan, found that low-intensity livestock grazing does not degrade habitat at the landscape scale (112) and has little to no impact on male abundance and female nesting success there (114, 214). Where captive-bred individuals have been introduced in Saudi Arabia, the birds generally remain almost entirely within the fenced reserve, presumably because of the better vegetation cover therein and lower levels of disturbance (70). In the wintering areas, the effect of habitat loss may be more

pronounced, with the conversion of habitat to agriculture considered a significant threat in Iran (215); although some bustards may exploit crops (139), they do require suitable native habitat within 6 km of agriculture (216).

Hunting

The main factor in this species' decline over the past 50 years has been sport hunting and poaching, both by firearms and falconry, the intensity and reach of which have greatly surpassed sustainable levels (217, 218). Photos of large takes are boasted about on social media, and the costs associated with this pastime can be high (218). Though hunting occurs mainly during the non-breeding season, falconers now also pursue this quarry at breeding areas and migration stopover points in Central Asia (219, 220, 186, 98). Throughout the species' range, between 1994 and 2000, the annual take was estimated to be three times the sustainable yield (188). More than 53% of winter mortality of Macqueen's Bustard breeding in Uzbekistan has been attributed to hunting (221). Estimates of annual take in Pakistan have numbered in the thousands for decades: 4,360 birds were killed by local and visiting hunters in winter 1982/83, and 4,955 in 1984/85; in addition, some 2,000 individuals trapped there were sold to the United Arab Emirates during 1986–1988 (141, 222, 191). During the 1990s, hunting in Pakistan took up to 7,000 individuals annually (92, 217).

Trapping

The principal motivation for trapping and international trade in this species is for use in training falcons, with large numbers gathered in Pakistan and Iran and shipped to Arabia (173,223,190); for example, in 2014 a shipment of 240 individuals was seized en route between Pakistan and Bahrain (224).

Collisions with Stationary/Moving Structures or Objects

Due to its visual ecology and flight mechanics, Macqueen's Bustard is prone to collisions with powerlines, and traditional mitigations such as bird-flight diverters do not perform well for this species (128, 209). The magnitude of this threat is expected to worsen as renewable energy infrastructure expands across the sunny, windy, and open habitats preferred by the species.

Management

Captive Breeding

Captive breeding has become an increasingly applied tool for the conservation of the Macqueen's Bustard with the aim of supplementing exploited populations as well as providing quarry for hunters and captive birds to train their falcons. First bred in the 1970s (150), it took two decades before mass breeding became possible at the scale required by demand (225, 226). Using artificial insemination, the species is now bred at the rate of tens of thousands per year, and released in very large numbers (94). This method of production requires a high level of docility among the breeding stock. Dolman et al. (94) also found reports that captive-bred birds in Asia and the Middle East showed concerning levels of tameness, occasionally even approaching vehicles and humans. Survivability of captive-bred and released birds in the United Arab Emirates is low (227), and while survivability into the autumn of juveniles released in Uzbekistan approached those of wild-born juveniles (210, 167), survival beyond their first full migration is substantially lower (23% versus 37%; 167) and there is evidence of altered phenology (124). Concerns have also been raised regarding releases of captive-bred

individuals with behaviors (resident versus migratory) or geographic lineages inappropriate to the site of release (94).

Priorities for Future Research

Priorities for Future Research

Large numbers of Macqueen's Bustard are bred in captivity via artificial insemination, and tens of thousands are released annually across most countries in the species' range. Few terrestrial species are managed in the wild using captive breeding at this scale, and many impacts of this strategy remain poorly undertstood. Knowledge concerning the extent to which these releases contribute to the creation of self-sustaining populations, or conversely, reduce the sustainability of wild populations through introgression of genotypes adapted to captivity, competition for resources, or other effects, would provide guidance for conservation efforts.

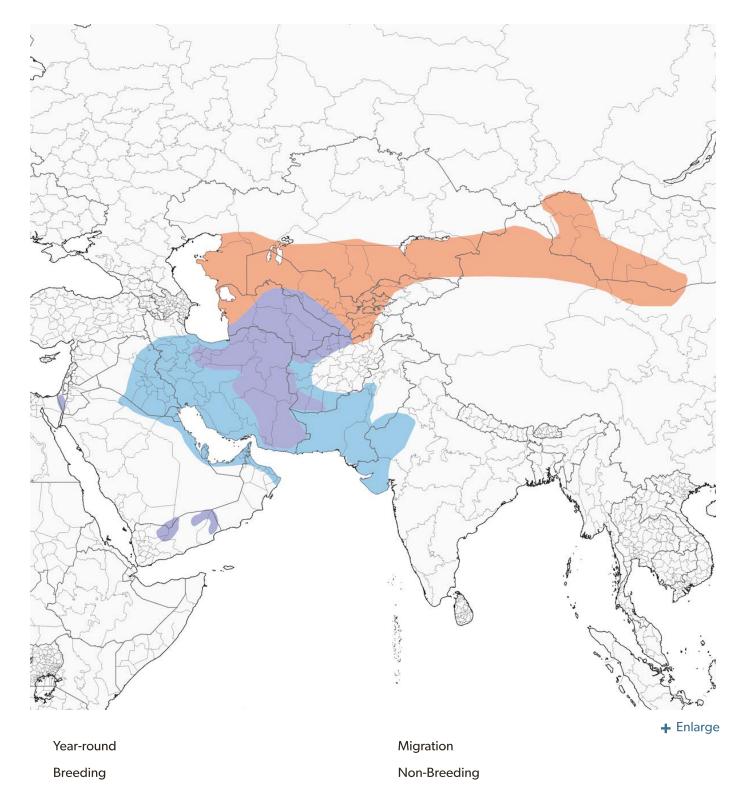
About the Author(s)

About the Author(s)

Dr Mimi Kessler serves as the Co-chair of the IUCN SSC Bustard Specialist Group. She earned a Ph.D. and M.Sc. in Biology from Arizona State University for spearheading a long-term program of ecological research and conservation policy on populations of the <u>Great Bustard</u> (<u>Otis tarda</u>) in Central Asia. Her professional work over 20 years in North Eurasia, South and Southeast Asia, and the Arabian Peninsula has extended to several other members of the bustard family. She has contributed to bustard conservation through successful proposals at four Conferences of Parties to the Convention on Migratory Species, and is actively engaged with the energy sector to reduce collisions, to which bustards are especially vulnerable. Email: mimi at eurasian bustard alliance.org

Dr Robert J. Burnside is a conservation biologist. He received his B.Sc. in Zoology from Imperial College, London, in 2004 and an M.Sc. in Conservation Biology from the University of Cape Town, South Africa, in 2007. He completed a Ph.D. in Reintroduction Biology at the University of Bath, UK, in 2013 with a thesis entitled "Conservation and Reintroduction of the Great Bustard *Otis tarda*". Since 2013 he has worked on the conservation, captive-breeding, release, and sustainable management of houbaras. Email: robertjohnburnside at hotmail.com

Dr Nigel Collar has worked for BirdLife International since 1981 in a variety of roles, and is currently the Leventis Fellow in Conservation Biology. He has served as Chair and is now Cochair of the IUCN SSC Bustard Specialist Group. Email: nigel.collar at birdlife.org



Distribution of the MacQueen's Bustard

Map last updated 21 August 2024.



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