allow a calibration of molecular clocks in many avian taxa. As both mutations in the cytochrome b segment are neutral transitions in third codon positions and calibration of the 16S rDNA is not definitely possible, we consider the two species as close relatives. Superspecies treatment, as suggested by Sibley & Monroe (1990), seems therefore appropriate.

The very restricted present ranges of Bald and Waldrapp Ibises are mostly the result of human impact on their populations (Collar & Stuart 1985; Hancock et al. 1992; Pegoraro 1996). Considering their historical distribution, possible habitats could have been much more widespread during the wettest parts of the interglacial periods when the Sahara was still a savanna and steppe landscape and lowland forest was much less widespread in Central Africa than it is today (cf. Louette 1992 and citations therein). A possible contact zone between the two species, or the distribution range of a hypothetical ancestral species, could be located in the mountain and savanna areas of Eastern and northeastern Africa. Postglacial changes of climate and vegetation could have resulted in the wide geographical split of the Geronticus ibises. The Wattled Ibis, *Bostrychia carunculata*, could be an isolated, possibly earlier lineage, closely related to the genus *Geronticus*. Data on breeding behaviour and ecology of this rare and range-restricted species are scarce, but the known facts (Hancock et al. 1992) indicate that it may be closely related to *Geronticus*. Its placement in the genus *Bostrychia* has been considered uncertain by several authors (cf. Hancock et al. 1992). As we still lack tissue samples and molecular data of this species, molecular evidence for the phylogenetic relationship of all cliff-breeding African ibises is still not available.

As the conservation status of the Southern Bald Ibis is much better than the situation of its northern relative, future conservation projects for the Waldrapp Ibises could benefit from the knowledge of the close phylogenetic relationship between these species. Therefore a comparative analyses of the conservation efforts may help to find a suitable strategy to ensure the survival of Waldrapp Ibises.

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**References**


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**Zusammenfassung**

gindiana, Lissotis hartlaubii, nomenclature follows del Hoyo et al. 1996) of semiarid and arid northern Africa and the Middle East. The difficulty in watching naturally behaving bustards has limited quantitative study of the group. Other methods of recording habitat use, location and abundance have been used, such as flushing birds while driving (e.g. Mian 1984; Seddon & van Heezik 1996), or locating and following footprints (e.g. Lauray et al. 1996). While valuable, these studies offer few data on sex-related differences in populations, and would be greatly enhanced if males and females could be reliably identified in the field.

At least 15 species of bustard are sexually dimorphic in body size, and although size alone is an unreliable method of sexing a flying or lone bird, footprint size should be a quantifiable sex-related characteristic in these species. Here, I test this prediction by measuring and comparing footprints of free-ranging Houbara Bustards, Chlamydotis (undulata) macqueenii Gaucher et al. 1996), of known sex.

Methods

Footprint measurements were made in Mahazat as-Sayd reserve (41° 45'N, 22° 10'E), Central Saudi Arabia. The Houbara Bustards in this study were all captive-reared and released at about two months of age each year from 1992 to 1997 (Combreau & Smith 1998; unpubl. data). All were fitted on release with back-mounted solar-powered transmitters with individual frequencies and could be located as required. All surviving Houbara Bustards were sexed as adults, 1–3 years after release, through direct observation of breeding behaviour (display behaviour for males, and nest building for females). Sample sizes were limited, because only 20% of Houbara Bustards released survived to breeding age when they could be sexed.

Foot measurements of five male and five female subadults (55–92 days after hatching) were obtained by allowing the bird to stand in a natural upright position on a sheet of paper during transmitter attachment prior to release, then marking the maximal length and width. Foot length was measured from the base of the posterior pad to the tip of the third anterior pad, excluding the claw. Foot width was measured as the greatest distance across the toe pads, excluding the claw (Fig. 1). Foot prints of nine male and 14 female adults (aged two years or more) were found by following radio signals emitted from the transmitter until the bird was seen. Houbara Bustards usually ran quickly from the vehicle when approached. Footprints of Houbara Bustards were relatively easy to locate because the birds frequently use or cross areas of silt, sand or fine gravel. Tracks of the bird were then back-tracked until the tracks indicated that the bird had been walking slowly. Distances between 'slow walking' tracks were usually less than two times the birds' foot length (about 10 cm maximum), whereas tracks of running birds could be separated by more than 50 cm and were always blurred in outline. To increase consistency, footprint measurements were only taken of birds that were walking slowly, in which the outline of the pads were clear and had well defined edges. For each adult the means of lengths and widths of a set of four to nine individual footprints were taken.

Comparisons of mean lengths and widths, and the ratios of foot length to width (calculated by dividing mean foot lengths by widths for each bird) were compared between sexes and within age groups using Mann-Whitney U tests. Four birds (three females and one male) were measured on each of two occasions, once when they were subadults soon after release, and once when they were adult. Footprints of these birds were compared using a Wilcoxon matched pairs test.

Results

Mean foot lengths and widths of wild adult male Houbara Bustards (n = 9) were an average of 22–23% larger than those of females (n = 14, Mann-Whitney U tests, p < 0.001; Fig. 1, Table 1). There was no overlap in foot lengths between the sexes, the smallest adult male foot length was 45.4 mm, 5% more than the widest female foot (43.4 mm). Apart from one outlying female (50.6 mm foot length), foot lengths of females were always less than 44.8 mm and males more than 47.6 mm. However, the ratio of length to width was similar between sexes, with ratios of about 1:1.08 for both males and females (U-test, P = 0.80; Table 1).

Subadult female foot lengths and widths (n = 5) were significantly smaller than those of subadult males (n = 5, U test, P < 0.05). Subadult footprints were similar in measurement to footprints of adult Houbara Bustards of the same sex (Fig. 1). The foot measurements of one male and three females taken both as subadult and adult were similar (Wilcoxon sign rank test, not significant, P > 0.05).

Discussion

The results show that the feet of male Houbara Bustards were an average of more than 20% larger than those of females, but both male and female feet are similar in shape. With one exception, foot lengths and widths of adult male and female in this population are non-overlapping. Furthermore, differences in footprint size between the sexes are discernible in birds that are as young as two to three months old.

Houbara Bustards younger than two months may not be readily sexed using this method, because feet of small males may overlap with larger foot sizes of older females. In addition, juveniles between the ages of about one and two months are problematic, as juvenile male foot sizes approximate those of adult females, and as juvenile female foot sizes remain very small. However, very young Houbara Bustards (less than one month old) have correspondingly small feet with footprints less than about 30 mm in length (unpubl. obs.), and so will not be confused.

Fig. 1. Lengths and widths of footprints of male (n = 9) and female (n = 14) Houbara Bustards. The inset shows the position on the footprint where width (horizontal arrows) and length measurements (vertical arrows) were taken.
with adult tracks, which are always >35 mm in length. Young Houbara Bustards (from hatching to several months of age) are always in close proximity to their mother, and this may aid identification of young during these few months. All other Houbara Bustards greater than a few months of age should be able to be reliably sexed using footprint measures, and all birds recorded from mid-summer (June) to late spring (February) will have footprint sizes that are full size and differentiable by sex.

While care was taken to record only walking tracks with clear pad impressions, these were frequently available in the reserve in a variety of habitats, including grass patches, open scrub of *Acacia* spp., wadis, and salt plains, and on substrata of sand, silt, and firm and loose gravels. The technique appears relatively robust and should have wide application for other species within the family, as most bustard species live in open semi-arid or arid grasslands and deserts, and most bustard species live in open semi-arid or arid grasslands and deserts, and are sexually dimorphic in body size. Confirmation that the technique is reliable for other Houbara Bustard populations and for other species is now required. I know of no other studies that have used footprints to reliably determine the sex in cursorial birds.

There are a number of avenues of research where sexing birds by their footprints could clarify aspects of Houbara and other bustard ecology, habitat use and social structure. In studies that follow footprints to determine habitat use and movements, comparisons between sexes may highlight differences in habitat requirements or utilization, and diet. Similarly, studies that estimate populations through counting birds (e.g. Mian et al. 1988) could use footprints to examine differences in detectability between males and females among seasons (for example, when the female is incubating she may not flush when a vehicle approaches and would therefore be 'missing' from density estimates). Workers who use tracks to locate nests (e.g. Maloney 1998) could initially determine the sex of the bird to avoid wasting long periods of time tracking male birds. Alternatively, male tracks could be followed to find display sites.

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**References**


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**Appendix**

**TABLE 1. Mean and standard deviations of male and female adult and subadult Houbara Bustard footprint lengths and widths (mm), the ratio of length to width (L/W), and range of measurements. Significant comparisons are given in the text.**

<table>
<thead>
<tr>
<th></th>
<th>Adult male</th>
<th></th>
<th>Adult female</th>
<th></th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Length</td>
<td>Width</td>
<td>L/W</td>
<td>Length</td>
</tr>
<tr>
<td>Mean</td>
<td>51.5</td>
<td>47.6</td>
<td>1.08</td>
<td>41.8</td>
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<tr>
<td>S.D.</td>
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<td>1.89</td>
<td>0.07</td>
<td>3.68</td>
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<tr>
<td>Minimum</td>
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<td>45.4</td>
<td>1.05</td>
<td>35.6</td>
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<tr>
<td>Maximum</td>
<td>58.3</td>
<td>50.8</td>
<td>1.17</td>
<td>50.6 (44.8)*</td>
</tr>
<tr>
<td>n</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>14</td>
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<table>
<thead>
<tr>
<th></th>
<th>Subadult male</th>
<th></th>
<th>Subadult female</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Length</td>
<td>Width</td>
<td>L/W</td>
<td>Length</td>
</tr>
<tr>
<td>Mean</td>
<td>49.8</td>
<td>44.0</td>
<td>1.14</td>
<td>45.4</td>
</tr>
<tr>
<td>S.D.</td>
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<td>1.14</td>
<td>0.06</td>
<td>1.67</td>
</tr>
<tr>
<td>Minimum</td>
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<td>43.0</td>
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<td>44.0</td>
</tr>
<tr>
<td>Maximum</td>
<td>52.0</td>
<td>56.0</td>
<td>0.93</td>
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</table>

*Maximum length measurement in brackets excludes the 50.6 mm outlier.