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Sexual size dimorphism in the Common Crane, a monogamous, plumage-monomorphic bird

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Male-biased sexual size dimorphism (SSD) is common and related to male mating success in polygynous birds, but also occurs in monogamous species, in which sexual selection can be strong. In these species, SSD in morphological traits not directly related to reproductive function, such as locomotory or feeding structures, has remained difficult to explain. We present the first biometric data of an archetypal monogamous bird, the Common Crane (*Grus grus*), based on molecular sexing techniques. Males were heavier and larger than females, with weight showing the largest SSD, followed by wing, central toe, and head length in adults and juveniles. These sexual differences were also present in nine crane pairs where both adults were measured, with values being positively correlated between pair members, suggesting assortative mating and female choice as the main mechanisms driving the evolution of SSD. Since central toes and bills are used as weapons during male-male combats, intra-male competition could also be involved as a sexual selection mechanism. Our results suggest that these small but significant sexual differences in certain morphological traits have probably evolved mainly through sexual selection in this monogamous, plumage-monomorphic species.

1. Introduction

While female-biased sexual size dimorphism (SSD) predominates in most vertebrate and invertebrate lineages, male-biased SSD is the most common pattern in birds and mammals (Fairbairn 2013). It has been studied mostly in polygynous species, and related primarily to the mating success of males (Payne 1984, Andersson 1994, Weckerly 1998, Fairbairn 2007, Alonso *et al*. 2009). However, studies investigating low to moderate SSD in monogamous, less dimorphic or plumage-monomorphic species are scarce, although sexual selection can be also strong in these species (Andersson 1994). Morevover, SSD in morphological traits not related to reproductive function, such as locomotory or feeding structures, has remained more difficult to explain than that of secondary sexual characters (Fairbairn 2007, Székely *et al*. 2007).

Like most monogamous birds, where competition over mates is limited, most crane species are monomorphic in plumage and show a low SSD. Male cranes are usually heavier and larger than females, although there is much overlap between sexes (Walkinshaw 1973, Johnsgard 1983, Archi-

bald & Meine 1996). Male cranes are typically the principal territory defenders, more aggressive against flock mates during foraging, and even take often the leading role when walking or flying (Johnsgard 1983; Tacha 1987; Swengel 1996; Alonso *et al*. 2004). These differences in the roles of both sexes suggest that males are still subject to sexual selection, and its effects could be reflected in the degree of sexual dimorphism of certain morphological structures used in agonistic encounters over territories and other resources relevant for mating.

Here we present the first biometric data of an archetypal monogamous bird with long-lasting pair-bond, the Common Crane (*Grus grus*). Male and female cranes live together throughout the year, foraging in pairs or mixed-sex flocks and sharing ecological niche, which excludes resource-division and sexual segregation as causes to explain SSD (Ruckstuhl & Neuhaus 2005). Our sample consists of 71 individuals sexed mostly through molecular techniques, and includes 9 pairs where both adults were measured.

We captured these cranes at Gallocanta lake, one of the main stopover sites in the western migratory route, where a large proportion of individuals stage during both, autumn and spring migrations (Alonso *et al*. 1984, 1987, 1994). Therefore, the data presented in this study can be taken as a representative sample of the biometry of the Common Crane population breeding in Scandinavia, central Europe, and western parts of Finland and the Baltic countries, and wintering in Spain, France, Portugal, and Morocco. This is the most numerous population of the species, with an estimated 350,000 individuals (Prange 2016).

Previously published biometric data on Common Cranes are mostly from small samples of museum skins (Table S1), and data from live individuals exist only for a Russian crane population breeding in Oka Nature Reserve, 230 km east of Moscow, and migrating through the eastern European route (Markin & Krever 1995, Winter *et al*. 2016). However, these cranes were sexed by their behaviour and not confirmed through molecular techniques. Although adult cranes can be generally sexed by their vocalizations (Walkinshaw 1949, Archibald 1976a,b), this sexing technique is not possible in all cases and cannot be used as a completely safe method. Safe methods are fecal steroid analysis, laparoscopy, karyotyping, measurement of total DNA content, and molecular sexing using DNA (van Tuinen & Valentine 1987, Swengel 1996). The aims of the present study were (a) to provide the first biometric data of the western population of the Common Crane based on molecular sexing techniques, and (b) discuss the possible role of sexual selection in the development of SSD in this species, based on sexual dimorphism in crane pairs with measurements from both adults, early development of SSD in juveniles, and behavioural observations from marked individuals.

2. Materials and methods

2.1. Capture methods

Between March 1988 and January 1992, 117 Common Cranes were captured at Gallocanta lake (NE Spain, 40°58' N, 1°30' W), using either a rocket net or alpha-chloralose. The net was a waterfowl-pigeon-dove net from Wildlife Materials Inc., Carbondale, Illinois, USA, measuring 19 × 10 m, with three rockets (for details see Wheeler & Lewis 1972). The alpha-chloralose was mixed with barley, wheat and corn as bait and following the usual procedures (Williams & Phillips 1973, Nesbitt 1976, Farhadpour 1987). Between 20 and 50 piles of baited grain were located at each capture site. Unbaited grain and stuffed cranes as decoys were also used to attract birds to the capture sites. The baited grain was always placed before dawn on the feeding grounds used by the cranes during the previous days. We avoided the proximity to drinking places in order to eliminate the risk of narcotized birds being drowned. The grain remained on the site during the whole day watched by 1 or 2 observers, who remained in radio-contact with the rest of the team.

Most cranes were captured during the morning foraging period, between 09:00 and 10:30h UTC. After capture we removed the remaining piles of baited grain before going to a building that we used as our field station, where we left the narcotized birds recover from the drug effects for 12–18 h in a dark room before processing them. Cranes captured with alpha-chloralose were released on the following morning, whereas those

Table 1. Definitions of the measurements taken on adult and juvenile Common Cranes. Linear measurements in mm, weight in g.

Wing arch	Maximum distance between the carpal joint and the tip of the longest primary, measured with a tape along the dorsal side of the wing
Wing chord	Minimum distance between the carpal joint and the tip of the longest primary feather (unflattened wing length)
Tail length	Length of the longest tail feather, pushing the bottom of the ruler gently against the base of the middle pair of tail feathers while the tail is folded naturally
Tarsus length	Distance between the notch on the back of the intertarsal joint and the lower edge of the last complete scale before the toes diverge
Central toe length	Distance between lower end of tarsus and Central Toe tip excluding the claw, with the toe stretched
Head length	Maximum distance between the occipital end of the head and the tip of the bill
Head width	Maximum width of the skull behind the eyes
Bill length (culmen)	Distance between the base of the skull and tip of the upper mandible
Bill length (nostril)	Distance between the posterior end of nostrils and tip of the upper mandible
Bill height	Distance from the culmen to the gonys at the proximal end of the culmen, where it reaches the base of the skull
Weight	Measured before release with a pesola (10 kg, 0.050 kg sensitivity)

captured with the rocket net were processed and released immediately. All birds were released close to nearby foraging or resting flocks, always in areas with good visibility and easy access as a precaution, in order to check that they had completely recovered and behaved normally.

All birds were provided with individual combinations of three self-made PVC (Gravoply) colour-rings for visual identification (1.6 mm thick, 20 mm inside diameter, 22 mm height), and with numbered metal rings, and 58 of them were additionally provided with transmitters from different manufacturers (models P2 and SB2, solar powered with activity sensor, AVM Instrument Co., Livermore, California, USA; model TW2, battery powered, 65g backpack or 25g leg-mounted, Biotrack Ltd., Dorset, UK). Leg-mounted transmitters were attached to a PVC leg-band, and backpacks were fitted with a two-loop teflon harness (model NOH, Telonics, Arizona, USA). The total weight of transmitters including attachment elements varied between 0.9% and 2.2% of the bird's weight. Radiotagged birds were observed in the study area for a period of 1–4 years to study their behaviour, using LA12-DS receivers and 3-element yagi antennas (AVM Instrument Co., Arizona, USA) (Alonso *et al*. 1997, 2004, Bautista *et al*. 1995, 1998).

2.2. Measurements taken

The morphological measurements taken are defined in Table 1. Plumage differences were used to distinguish adults (here we include in this age class all birds older than 1 year) from juveniles (first year birds). Weight was measured to the nearest 50 g using a 10-kg Pesola scale. Wing arch, wing chord, and tail lengths were measured to the nearest 1 mm, and all other measurements were measured to the nearest 0.1 mm. All measurements were made by the same person.

2.3. Sexing methods

In total, 71 of the 117 cranes captured were sexed, either through molecular techniques using their Giemsa-stained blood smears (24 adults, 28 juveniles), display or mating behaviour (17 adults), or necropsy (1 adult, 1 juvenile). Blood samples (1 ml) were originally collected for hematological analyses from the brachial vein of 74 of the 117 captured birds using heparinized syringes (25 U/ml) (Puerta *et al.* 1990, Abelenda *et al*. 1993). In addition, blood smears were also made and fixed through 3 min immersion in methanol at the time of blood collection. They were stained with commercial Giemsa stain (Merck, Germany) diluted in phosphate buffer (1: 4.5) pH 6.8 for 45 min.

Table 2. Measurements of Common Cranes captured and ringed at Gallocanta lake, Spain. The age category "adults" includes all non-juvenile individuals. Linear measurements in mm, weight in g.

	Adult males				Adult females				Juvenile males				Juvenile females			
	Mean	*SD*	Min–max	*n*	Mean	*SD*	Min–max	*n*	Mean	*SD*	Min–max	*n*	Mean	*SD*	Min–max	*n*
Wing arch	608.9	17.4	580.0–650.0	21	574.5	27.8	520.0–625.0	20	572.1	11.9	545.0–590.0	18	557.4	14.8	525.0–580.0	11
Wing chord	559.5	20.6	530.0–600.0	21	532.1	24.9	485.0–580.0	21	526.2	14.8	510.0–557.0	18	515.9	21.7	475.0–545.0	11
Tail length	214.3	9.1	195.0–230.0	21	202.9	9.1	190.0–220.0	21	186.8	8.4	170.0–200.0	18	181.6	7.0	170.0–190.0	11
Tarsus length	253.6	11.4	231.0–278.0	21	244.0	14.3	220.0–268.0	21	251.2	13.3	230.0–278.0	18	242.8	5.8	233.0–250.0	11
Central toe length	99.9	3.2	95.0–108.5	21	94.8	4.5	86.0–103.1	21	97.0	4.5	84.2–102.6	18	93.3	3.5	89.5–100.6	11
Head length	186.0	5.1	175.6–195.0	20	177.9	5.8	169.0–188.4	21	180.8	4.9	173.5–189.3	18	174.6	5.6	167.8–187.0	11
Head width	44.6	1.2	42.2–46.8	21	42.9	1.2	41.0–45.0	21	43.5	1.6	40.3–45.9	18	42.1	1.1	41.0–44.3	11
Bill length (culmen)	107.5	5.6	95.3–119.0	21	103.9	4.3	95.8–112.5	21	105.2	4.4	96.1–112.4	18	101.5	4.4	93.3–109.5	11
Bill length (nostril)	77.6	4.0	68.5–84.8	21	74.4	4.0	68.5–82.0	21	75.0	2.6	71.4–80.7	18	70.6	4.3	61.6–79.2	11
Bill height	31.8	1.4	30.0–34.6	21	31.0	1.6	27.3–34.6	21	31.0	1.5	27.5–33.8	18	30.2	1.4	28.4–31.9	11
Weight[1]	5,929	373	5,250–6,550	21	5,150	413	4,450–5,800	21	5,075	369	4,250–5,600	18	4,732	522	4,200–5,850	11

1) This sample does not include maximum weights of 7,500 g (adult bird, the maximum weight ever recorded) and 6,300 g (juvenile), of two individuals that could not be sexed. Both birds were the heaviest ever recorded for Common Cranes in their respective age classes (see Table S1), and also largest, as shown by their linear measurements. Adult: wing arch 660, wing chord 601, tail 235, tarsus 266, central toe 113.5, head length 201.1, head width 45.0, bill length (culmen) 119.6, bill length (nostril) 85.8, bill height 36.0; juvenile: wing arch 620, wing chord 560, tail 200, tarsus 262, central toe 112.4, head length 184.7, head width 43.5, bill length (culmen) 110.0, bill length (nostril) 75.3, bill height 30.9.

Table 3. Significance of morphometric differences (Student's t-test) between sexes and sexual size dimorphism indices (SSD%) in adult and juvenile Common Cranes. Sample sizes for each sex are given in Table 1.

	Adults				Juveniles			
	t-value	*df*	*p*	SSD%[1]	*t*-value	*df*	*p*	SSD%[1]
Wing arch	4.79	39	0.000	6.0*	2.91	27	0.007	2.6
Wing chord	3.90	40	0.000	5.2*	1.55	27	0.133	2.0
Tail length	4.05	40	0.020	5.6*	1.68	27	0.104	2.9
Tarsus length	2.42	40	0.000	3.9	1.93	27	0.064	3.5
Central toe length	4.23	40	0.000	5.4*	2.28	27	0.031	4.0*
Head length	4.74	39	0.000	4.6*	3.15	27	0.004	3.6*
Head width	4.62	40	0.000	4.0	2.52	27	0.018	3.3
Bill length (culmen)	2.32	40	0.026	3.5	2.16	27	0.040	3.7*
Bill length (nostril)	2.60	40	0.013	4.3	3.42	27	0.002	6.2*
Bill height	1.81	40	0.078	2.6	1.35	27	0.188	2.7
Weight	6.31	40	0.000	15.1*	2.18	27	0.038	7.3*

1) Sexual size dimorphism indices (SSD%) were calculated as 100*(male value–female value)/female value; SSD% values higher than the mean SSD% of all linear measurements (= 4.49 in adults, 3.43 in juveniles) are marked with an asterisk.

DNA could be extracted from 52 samples, and the sex of these individuals could be determined in spite of the highly degraded state of the samples, thanks to a newly developed technique to select new sex-specific primers that can now be used for any bird species (Morinha *et al*. 2018). DNA could be isolated from the Giemsa-stained blood smears using the Quick-DNA Miniprep Plus Kit (Zymo Research).

For a reliable molecular sexing of these samples, we selected a new female sex-specific marker to amplify short DNA fragments. Primers were selected based on CHD1Z and CHD1W sequences available for cranes (GenBank IDs: EU814903 and EU814910). PCR was performed in multiplex using the female sex-specific primers CRANE-F (5'-CGTCAGTTTCCCTTTCAGGTA-3') and CRANE-R (5'-AAGTGGTAAAGATCAAGGCTTCT-3') that amplify a fragment of 66 bp only in females, and the primers sfsr/3Fb (5'-ACTAGCCCTTTCAGCGTCATGT-3') and sfsr/3Rb (5'-CATGCTCGGGAACCAAAGG-3') (Bejerano *et al*. 2004) that amplify a ultra-conserved element of approximately 114 bp in both males and females.

PCR amplifications were performed in a volume of 10 µl, containing 5 µl of Supreme NZYTaq 2× Green Master Mix (NZYTech), 2.5 pmol of each primer and 2 µl of genomic DNA. The thermal protocol consisted in a initial denaturation at 95 ºC for 5 min followed by 35 cycles of 95 ºC for 30 s, 58 ºC for 1 min, 72 ºC for 30 s and a final extension at 60 ºC for 10 min. PCR products were separated by electrophoresis on 3% agarose gels (see details in Morinha *et al*. 2018).

In the course of behavioural observations of marked cranes the sex of 25 adult individuals could be determined through their sex-specific postures and antiphonal duetting calls during the unison-call display (Walkinshaw 1949, Archibald 1976a,b, Swengel 1996).

We conserved blood samples from eight of these 25 individuals, and in all cases sex determined by behavior was later confirmed by molecular sexing.

2.4. Statistical analyses

We analyzed sex differences using two-sample Student's *t*-tests on log-transformed variables. To test male-female differences of the same pairs, we used Wilcoxon's matched-pairs test. Assortative mating by morphological measurements was explored through bivariate Pearson correlations (Barbraud & Jouventin 1998, Einoder *et al*. 2008, Carey 2011, Bourgeois *et al*. 2017). We used STATISTICA, version 6.0 (StatSoft, Tulsa, Oklahoma), for these analyses, and all tests were two-tailed (Statsoft Inc. 2001).

Table 4. Significance of morphometric differences (Wilcoxon matched pairs test) between sexes and sexual size dimorphism indices (SSD%) in 9 Common Crane pairs where both adults were measured.

	Z	*p*	Male > female[3]	Female > male[3]	Male = female[3]	SSD%[4]
Wing arch	1.89	0.059	6	2	0	5.4
Wing chord	2.01	0.044 *	7	2	0	4.6
Tail	2.11	0.035 *	6	1	2	5.7
Tarsus length	1.48	0.139	6	3	0	5.7
Central toe length	2.43	0.015 *	8	1	0	6.3*
Head length	2.67	0.008 **	9	0	0	6.8*
Head width	2.19	0.028 *	7	2	0	3.7
Bill length[1]	2.67	0.008 **	9	0	0	7.1*
Bill length[2]	2.67	0.008 **	9	0	0	7.9*
Bill height	1.84	0.066	8	1	0	4.8
Weight	2.67	0.008 **	9	0	0	15.5*

1) Culmen
2) Nostril-extreme
3) Number of pairs where male value was higher, lower or equal to female value
4) Sexual size dimorphism indices (SSD%) were calculated as 100*(male value–female value)/female value; SSD% values higher than the mean SSD% of all linear measurements are marked with an asterisk.

3. Results

All measurements were larger in males than females of both age classes, except bill height in both ages, and wing chord, tail and tarsus length in juveniles, where differences did not reach significance (Tables 2 and 3). In adults, the largest differences between sexes were found in weight (males were 15% heavier than females), followed by the lengths of wing, tail, central toe, and head length, which showed SSD values above average for all linear measurements (Table 3). Sexual differences were less pronounced in juveniles, and highest also in weight, followed by bill, head and central toe lengths (Table 3).

These sexual differences were also found in the subsample of crane pairs where both adults were measured. Except tarsus length and bill height, males showed larger morphometric values than their female mates (Table 4). Wing arch was only marginally larger in males probably due to the missing value in one of the pairs (8 instead of 9 values, Table 4), but the difference in wing chord did reach significance. Weight, head length and bill length were the only measurements where all nine males showed higher values than their female mates, and so reached highest significance values ($p < 0.01$). Together with central toe, which was also larger in most males (8 of 9 pairs, $p < 0.01$), these four measurements showed the highest magnitudes in SSD (Table 3). In pairs, male and female measurements were significantly correlated (weight: $r = 0.71$, $p = 0.03$; bill length-culmen: $r = 0.71$, $p = 0.03$; bill length-nostril-: $r = 0.79$, $p = 0.01$; central toe length: $r = 0.67$, $p = 0.05$), suggesting that mating is assortative based on these measurements.

Juvenile cranes in their first winter had almost reached the size of adults (average for all linear measurements: 95.8% in males, 96.8% in females), but were still lighter (85.6% in males, 91.9% in females). Tails were by far the shortest linear measurements in juveniles compared to adults (12.83% shorter in males, 10.50% in females).

The differences among age and sex classes show similar patterns for weight and wing length, with adult males clearly outranking adult females, juvenile males showing similar values to adult females, and juvenile females showing the smallest values (Fig. 1). A slightly different pattern is found in tarsus, central toe, head and bill, where juvenile males showed similar or higher values than adult females (Fig. 1).

4. Discussion

The biggest morphometric difference between males and females was found in weight. Males

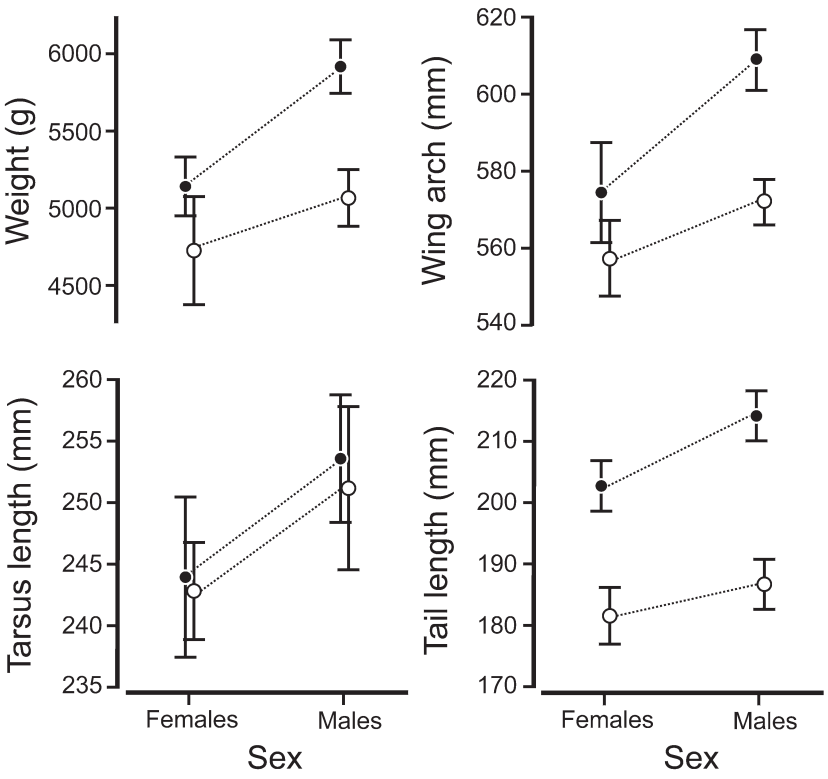

Fig. 1. Differences among sex and age classes (adults: black dots, juveniles: open dots) in weight, and wing, tarsus and tail lengths (means ± 95% CI). Differences in head length and width, bill length, and central toe length showed a similar pattern to that of tarsus length.

were 15.1% heavier than females in the sample of all adults and a 15.5% heavier than their female mates in the sample of pairs with measurements from both adults. A heavier weight represents an advantage in fending off nest predators or in fights with conspecifics over food, where larger birds are dominant in aggressive encounters, displacing smaller, subdominant individuals from good feeding sites. In our study with marked birds, males had the highest dominance ranks in winter flocks, and displaced other cranes from the best feeding sites, increasing their own intake rates (Bautista *et al*. 1995, 1998). In addition, males are more involved than females in territorial defense against predators and neighbor territory holders at both, nesting and wintering territories, whereas females spend more time taking care of their offspring (Nowald 2002, Alonso *et al*. 2004, Prange 2016). On the other hand, weight is limited by the energetic costs of migration in migratory crane species (Jones & Witt 2014). Therefore, while a large size and heavy weight may have primarily evolved as a balance between opposing natural selection forces in both sexes, sexual selection has probably favored higher male weights and more pronounced SSD. Females that mate with larger males benefit from both, the higher success of their mates in territory defense, and access to better feeding sites within foraging flocks during the non-breeding season.

The highest SSD in weight compared to linear measurements seems to be the rule within the crane family (Blackman 1971, Murata *et al*. 1988, Swengel 1992, Hartup & Horwich 1994, Fox 1995, Inoue *et al* 2013; see also published values for Common Cranes in Table S1), and the degree of SSD does not seem to be related to any taxonomic, ecological or geographical patterns within the crane family (Swengel 1992, Jones & Witt 2014). These results support that sexual selection has contributed to develop a heavier male weight in all crane species, independently of any natural selection pressures. However, the relative importance of SSD in weight compared to linear measurements should not be exaggerated, since body mass is directly related to body volume and thus a three-dimensional trait, whereas lengths of wing, tarsus, or bill are single-dimensional, so a SSD

factor of z in a linear trait would correspond to z^3 in weight (Fairbairn 2007).

Larger wings and tails are needed to support a heavier weight during flight, thus wing and tail sexual differences have probably evolved essentially through natural selection. This is also supported by Swengel's (1992) interspecific comparison, where the magnitude of linear measurement dimorphism was greatest in those species that had the most weight dimorphism. When comparing mean values among sex and age classes, the differences in wing length show a very similar pattern than those in weight, supporting the idea that wing dimensions have basically evolved as adaptations to support weight in flight. Juvenile males weigh slightly less than adult females and also have slightly shorter wings. In contrast, the tail is much less developed in juveniles of both sexes than in adults, and it is significantly longer in adult males than in adult females. The tail is used together with the tertials as a dominance character during agonistic and mating displays (Walkinshaw 1973; see arching, bowing, duetting, leaping and throwing postures in Masatomi & Kitagawa 1975). Its full development is thus unnecessary during the first year of life. Moreover, shorter tails may help juveniles show their subordinate rank and so evade many attacks from adults.

As for central toe, tarsi, and bill, they are used by both sexes in aggressive encounters between flock mates at wintering areas, where large males are usually dominant (Alonso *et al*. 1997, Bautista *et al.* 1995, 1998), and also represent fundamental weapons during male-male combats. Contenders exchange rapid thrusts of the bill ("bill-stab" in Ellis *et al*. 1998; "upright- and forward-pecking" in Masatomi & Kitagawa 1975), or leap into the air and slash at each other with their talons ("jump-rake" in Ellis *et al*. 1998; "kicking" in Masatomi & Kitagawa 1975). Their use as weapons during male-male encounters suggests that their male-biased SSD has evolved through intra-male competition, the first main mechanism of sexual selection.

Several results from this study support the evolution of SSD in these traits through sexual selection. First, in the nine pairs with measurements for both sexes, head, bill, and central toes were consistently longer in males, and showed the highest SSD magnitudes among all linear structures. Male and female measurements for these traits as well as for weight were correlated, indicating assortative mating. In 20 Brolga pairs (*Antigone rubicunda*), Blackman (1971) also found that males were always heavier and had longer heads, tarsi and larger bodies than their mates.

We suggest that females probably tend to choose mates larger than themselves, and that female choice, the second main mechanism of sexual selection, could also be important in maintaining SSD in these body structures. Sexual differences in bill size and shape and assortative mating in bill measurements within pairs have also been interpreted as a result of sexual selection in other plumage-monomorphic birds with low general SSD (Barbraud 2000, Babbitt & Frederick 2007, Einoder *et al*. 2008, Greenberg *et al*. 2013, Rico-Guevara & Araya-Salas 2015, Bourgeois *et al*. 2017, Fuchs *et al*. 2017).

In seabirds, where all species are monogamous, sexual selection is more influential on SSD than fecundity selection and natural selection mechanisms like niche-utilization, although the influence was weaker than in other bird groups with higher SSD like bustards or shorebirds (Serrano-Meneses & Székely 2006). The central toe represents a particular case where both, natural and sexual selection may have contributed to its marked SSD. Its stability-providing function during standing or walking certainly suggests that natural selection may have also played a significant role.

Second, SSD indeed develops at an early age in Common Cranes. We showed that 7–8 months old juveniles already showed the highest SSD magnitudes specifically in weight, bill length and central toe length, the three characters whose marked SSD has probably evolved through sexual selection. Indeed, male chicks are already significantly bigger and heavier than female chicks at the age of only a few weeks (J. C. Alonso, J. A. Alonso and G. Nowald, unpubl. data).

Third, the remarkable fact that juvenile males have longer bills and central toes, and bigger (longer and wider) heads than adult females supports the idea that the size of these structures in males has an important evolutionary component of sexual selection that makes them grow at an early age beyond the size of their mothers, whereas other structures like wing or tail, not used as arms in

agonistic encounters, don't grow so fast and are smaller in juvenile males than adult females.

Finally, it is interesting that central toe length and bill length were the linear measurements showing the highest SSD also among juveniles, supporting that the SSD in these characters might be the result of an evolutionary mechanism independent from that operating in other biometric features. Alternatively, a more parsimonious explanation would be that tarsus and central toe lengths develop early in juvenile males compared to juvenile females as an adaptation to the higher weight they will reach during adulthood.

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Sukupuolten kokoerot näennäisesti monomorfisella lajilla, kurjella

Sukupuolten kokoerot ovat yleisiä, ja koiras on usein kookkaampi sukupuoli. Kokoerot voivat liittyä koiraiden lisääntymismenestykseen polygynisillä lajeilla, mutta ilmiötä havaitaan myös monogaamisilla lajeilla, joilla seksuaalivalinta on voimakasta. Tällaisilla lajeilla kokoerot eivät suoraan liity lisääntymiseen, kuten ravinnonhankintaan tai liikkumiseen, ja ovat täten pulmallisia ymmärtää.

Tässä tutkimuksessa esitämme monogaamisten lajien esikuvan – kurjen – ensimmäisen biometrisen datan, jossa sukupuolet on määritetty molekyylimenetelmin. Havaitsimme, että koiraat ovat naaraita painavampia (sekä nuoret että aikuiset linnut). Suurin sukupuoliero oli juuri painossa, toiseksi suurin siivessä, sitten keskivarpaassa ja pään pituudessa. Samat erot havaittiin myös yhdeksällä kurkiparilla, joista mitattiin molemmat sukupuolet.

Parin mittaustulokset korreloivat positiivisesti, mikä antaisi ymmärtää, että pariutuminen on valikoivaa (naaras valitsee koiraan), mikä taas voi selittää sukupuolierojen evoluutiota. Koska keskivarpaat ja nokka ovat koiras–koiras-kilpailussa käytettäviä aseita, sukupuolierot voisivat viitata myös siihen että koiras–koiras-kilpailu, osana sukupuolivalintaa, voisi selittää kokoeroja. Tuloksemme viittaavat siihen, että pienet, mutta merkittävät erot sukupuolten välillä ovat kehittyneet sukupuolivalinnan seurauksena.

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Online supplementary material

Supplementary Table 1. A review of previously published Common Crane biometric data.