Report on *Ex situ* Kori Bustard Breeding and Behavior

Sara Hallager[1], Jeanette Boylan[2], Deborah Fripp[3], & Lauri Torgerson-White[3]

Running Head: Kori bustard report

[1]Sara Hallager, corresponding author
Smithsonian National Zoological Park, 3001 Connecticut Ave, Washington DC 20008
(p) 202-633-3088; email hallagers@si.edu

[2] Jeanette Boylan
Tarrant County College, Fort Worth, Texas

[3] Deborah Fripp
Darwin's Ark: Research Consulting and Coordination, Carrollton, Texas

[3]Lauri Torgerson-White
Darwin's Ark: Research Consulting and Coordination, Carrollton, Texas

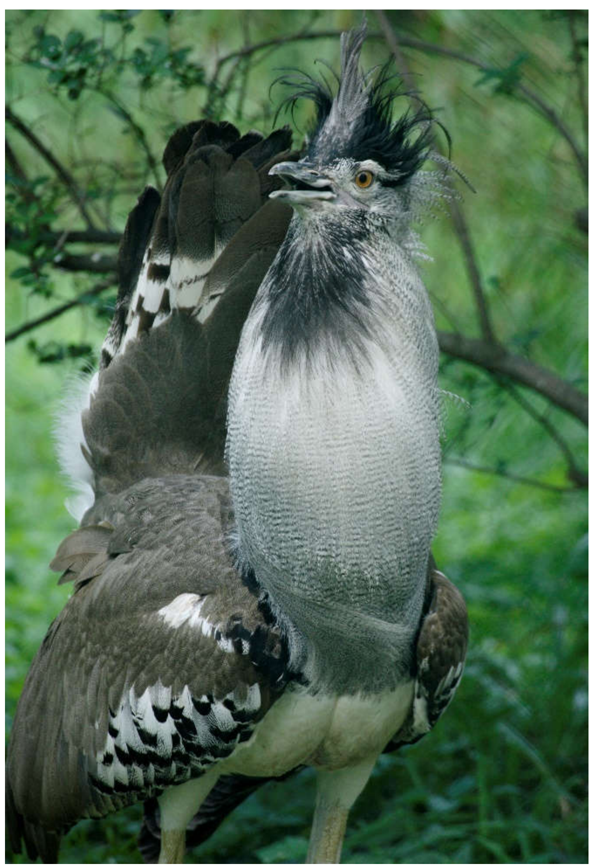


Photo by Jessie Cohen

Executive Summary

In 2007, the kori bustard Species Survival Plan (SSP) sponsored a behavioral study on *ex situ* kori bustards housed at nine institutions in the United States. Over 75,000 behavioral observations were collected on 50 birds over five years using the Colonel Stanley R. McNeil Foundation's EthoTrak Observation System, a Palm®-based program. These data were used to investigate three areas of interest and to make management recommendations.

How do kori bustards spend their time?

An ethogram of 31 behaviors organized into seven categories was adapted for the EthoTrak study from a pre-existing kori bustard ethogram. Analysis of the data generated overall activity budgets, which were compared for males vs. females, juveniles vs. adults, and breeding vs. non-breeding seasons. The kori bustards spent most of their time resting, as well as large amounts of time walking, performing body maintenance (e.g. preening), and feeding. Kori behavior differed significantly by age, sex, and season.

Does social housing impact breeding behavior?

The EthoTrak data in combination with institutional egg logs were used to investigate whether adult kori bustard breeding behavior was affected by the presence of same and opposite-sex conspecifics, heterospecific birds, and humans.

Male sexual behavior was the primary factor in whether females laid at all, but one of many factors in how many clutches a female laid. Male sexual behavior did not impact how much maternal behavior a female showed. The strongest impact on how many clutches a female laid and how much maternal behavior she showed came from the institution, with specific factors difficult to tease out of that effect.

Dominant males did not appear to interfere with displaying by other males. In fact, there was a trend toward multiple males stimulating each other to display. The strongest effect on male sexual behavior was the presence of other species of birds: males in exhibits with other species of birds performed significantly fewer display behaviors than males in kori-only exhibits.

Do hand-reared and parent-reared birds have equivalent survival and breeding success?

The EthoTrak data were combined with studbook data and data from a separate study on hand-reared chick behavior to investigate whether the choice to hand- or parent-rear kori bustard chicks impacted the chicks' future survival or breeding success. Both hand-rearing and parent-rearing of kori bustards were equally successful methods of producing chicks that survived to be successfully breeding adults. Hand- and parent-reared chicks behaved equivalently as chicks and adults. Chicks born to hand-reared and parent-reared birds survived to adulthood at equivalent rates to each other and to chicks born to wild-caught birds.

Management Recommendations

More research is needed to tease out the details of all of the results presented here. With that caveat, this research suggested the following recommendations:

- For institutions holding a pair that are not breeding, housing a second male in acoustic contact may stimulate more display behavior and lead to higher breeding success.
- Females in visual contact may have higher breeding success than those housed without other females or housed in physical contact.
- Managers should exercise caution when housing kori bustards with other bird species.
- Parent-rearing is acceptable, especially when staffing and resources are limited and predation is not an issue.

Table of Contents

1. General Introduction

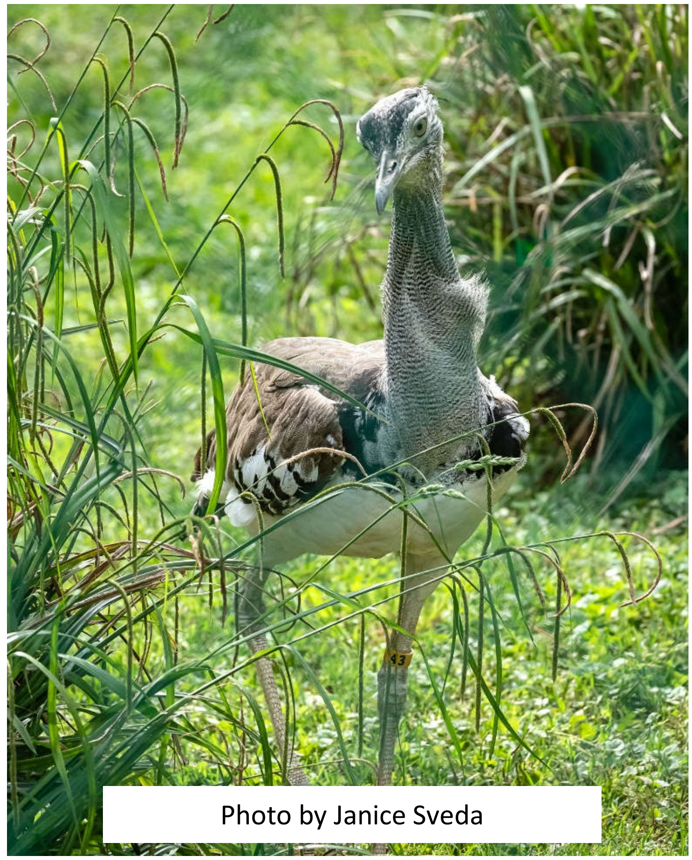


Photo by Janice Sveda

A flagship species for Old World grasslands, a recent analysis by BirdLife demonstrates that bustards are one of the most threatened terrestrial family of birds on earth (Collar personal communication 2020). The 25 species of bustard native to Africa, Asia, Australia, and Europe face growing pressures to survive including disturbance, habitat loss, hunting, collisions with powerlines, coupled with a low awareness by most people of the very existence of these taxa. A low awareness of bustards with key decision makers that could positively affect bustard conservation has certainly not helped the situation.

Those dedicated individuals that work and study with bustards both *in situ* and *ex situ* know their appeal, their beauty, their magnificence, and importance to the ecosystem. In human care, bustards have an undeserved reputation as being hard to breed and keep but cracking the code of bustard breeding can be accomplished by simply taking the time to understand their needs.

One of the largest of bustard species is the kori bustard, a large, mostly terrestrial bird indigenous to the grasslands and lightly wooded savannas of southern and eastern Africa (Senyatso *et al*., 2012). The species is suspected to be undergoing moderately rapid population declines across much of its range owing to a variety of threats including collisions with power lines, hunting, and habitat degradation. It has consequently been listed as Near Threatened by IUCN (Birdlife International, 2016).

Since 1993, a breeding program for the kori bustard in the United States has been managed under the auspices of the Association of Zoos and Aquariums (AZA) as a Species Survival Plan® (SSP). The kori bustard SSP program aims to maintain a population that is genetically and demographically self-sustaining without relying on continued imports from the wild. Currently, the population is experiencing a decline in interest by holding institutions and therefore a significant decline in breeding opportunities. At just under 40 birds, the species is in danger of vanishing from AZA zoos within the next 10-15 years (Hallager personal observation 2021).

Their reputation as a challenging species has contributed to this decline (Hallager, personal communication, 2021). However, a greater understanding of kori bustard interactions with conspecifics, heterospecifics, humans, and the environment is necessary in order to improve the husbandry and management of kori bustards in AZA zoos and convince managers that kori bustards can be an important, appealing and viable species to exhibit.

In 2007, it was clear that a greater understanding of kori bustard management was needed to improve reproduction and increase the captive population. A new tool available at the time called EthoTrak was employed and data collection began in several US zoos to understand the key factors necessary for successful breeding of kori bustards managed in human care.

The primary goals for this study were to:

1) document the onset of sexual maturity in males and females,

2) understand the behavioral effects of dominant males on subordinate males,

3) examine the behavioral effects of dominant females on subordinate females,

4) determine the effects of moving individuals between institutions.

Secondary goals of the project were to:

1) determine activity budgets for each sex, for adults vs. juveniles, and for breeding vs. non-breeding season,

2) understand how birds utilize exhibit space,

3) understand the effect of crowd levels on activity, and

4) evaluate the breeding success of hand-reared vs parent reared birds.

The study period ran for five years. Due to design limitations, not all goals were accomplished, but the study yielded numerous results which shed light on kori bustard management in an *ex-situ* setting. The results of this study are presented in this report.

Most zoos that acquire kori bustards soon discover they are charismatic and wonderful exhibit birds. Guests are visually drawn to them for their size, their impressive breeding displays and their unique appearance. Kori bustards offer an avian gateway for spreading the message about grassland conservation of many African species. If your facility does not currently house kori bustards, please consider this species. You will be a true conservation hero in the fight to save bustards.

2. Activity Budgets & EthoTrak Summary

2.1 Methods

Study Population

Nine AZA accredited institutions were involved in this study: Birmingham Zoo (BZ), Cheyenne Mountain Zoo (CMZ), Dallas Zoo (DZ), Living Desert Zoo (LDZ), Phoenix Zoo (PZ), Smithsonian National Zoological Park (SNZP), White Oak Conservation Center (WOCC), Zoo Atlanta (ZA), and Zoo Miami (ZM). The animal care staff at these nine zoos collected data on 50 birds, more than three-quarters of the US population (18 adult females, 14 adult males, 8 juvenile females, and 10 juvenile males). Birds were observed daily between 2007 and 2012. Adulthood was designated as three years, which is the youngest age at which kori bustards have been documented breeding in human care (Hallager, 2016).

Data Collection

Observational data were collected by keepers using the Colonel Stanley R. McNeil Foundation's EthoTrak Observation System (Watters *et al*., 2009), which used a Palm®-based program to collect behavioral data. Single point samples were taken on each individual three times per day between 8:00 and 15:00. Observers were instructed to mark a bird's behavior when they first observed the bird. Observers were permitted to take observations outside these times as well. Although there were data points recorded at all hours, data were collected in a consistent manner from all zoos between 7:00 and 17:00, and the data set was therefore restricted to observations collected during those hours.

To keep observations between facilities comparable, keepers at all facilities were trained in data collection by the authors (S.H. and J.B.) during in-person meetings, and a weekly schedule was developed (Table 1). Observations were taken at any time during the scheduled hour. During this time window, at least one observation was recorded for each animal. Additionally, the keepers could carry the Palm® with them and take additional observations when possible during their daily routine. To reduce bias of keepers noticing active behaviors, keepers were instructed to collect data without knowing what the birds were doing. Observations were not to be taken 15 minutes prior to or 30 minutes after scheduled feedings to allow the birds to finish eating and minimize an overabundance of feeding observations. If an animal was not visible, then no data were collected.

Table 1. Schedule of times of data collection.
Data was taken any time within the hour time block.

Time	S	M	T	W	Th	F	S
8:00-9:00			X		X		X
9:00-10:00		X		X		X	
10:00-11:00	X		X		X		
11:00-12:00		X		X		X	
12:00-13:00	X				X		X
13:00-14:00		X		X		X	
14:00-15:00	X		X				X

Ethogram

An ethogram of 31 behaviors organized into seven categories was adapted for the EthoTrak study from a pre-existing kori bustard ethogram (Lictenberg and Hallager, 2006; Table 2).

Table 2. Ethogram used in collection and analysis of EthoTrak study

ANALYSIS CATEGORY	
Recorded Behavior	**Description**
ALERT	
Rest Alert	Stationary, head up.
NOT ALERT	
Rest Not Alert	Stationary, head tucked.

LOCOMOTE	
Walk	Move about at a leisurely pace.
Pace	Walk back and forth, moving faster than when walking.
FEED	
Feed	Search for food while walking and looking down at the ground, peck at food, or chase down jumping or flying prey.
BODY MAINTENANCE	
Body Maintenance	Scratch, stretch, body fluff, ruffle, wing flap, preen, or bill wipe.
SUNBATHE	
Sunbathe	Sit in the sun with one or both wings spread horizontal to the ground.
PREDATOR AVOIDANCE	
Skyward Look	Extend head and cock it upwards, while alert. May also tilt head sideways so only one eye is facing upwards.
Neck Fluff	Neck feathers and/or the head crest erect.
SOCIAL-ANTAGONISTIC	
Aggressive Displacement	Chase another bird, generally with head lowered, head crest raised, plumage slightly ruffled, and body aimed towards the other but tail is not raised. The second bird vacates its position.
Non-aggressive Displacement	Walk toward another bird and the second bird vacates its position and moves elsewhere.
MATERNAL (FEMALE)	
Egg Turn	(Female) Rotate eggs with bill, while standing over the nest.
Incubate/Brood	(Female) Sit on eggs in the nest or chicks. May occasionally throw leaf litter and small sticks onto her back while incubating. *Because only females at DZ had the opportunity to sit on chicks, brooding of chicks was excluded from the analysis of this behavior.*
Offer Food	*(Female) Offer food to a chick. – this behavior was recorded but not analyzed as only females at DZ were permitted to raise their own chicks, and therefore had the chance to perform this behavior.*
SEXUAL (MALE)	
Balloon Display	(Male) Extend neck and inflate pouch (fully or partially) with the bill pointed upward. Tail and wing feathers are pointing downward and head crest is erect.
Boom	(Male) Give low-pitched, up to 6-note vocalization (with balloon display).
Chase Female	(Male) Run after a female with head crest and tail raised.
Copulate	Male pecks the back of sitting female's head. As copulation nears, male sits down and continues to peck at the female's head. Male spreads wings and climbs onto back of seated female. Just after sperm transfer, both birds stand and shake their feathers.
Head Toss	(Male) Toss head back quickly until the back of head touches the back.
Tail Up	(Male) Stand or strut around, with tail raised and fanned, wings held close to the body, and head crest erect.

OTHER (<1% of total)	
Chick Feed	(Chick) Accept food offered by dam.
Drink	Consume water.
Dust Bathe	Lie flat and rub belly, head, neck and wings on the ground, often in a sandy or dusty depression. Often accompanied by ruffling feathers in the sand or dust.
Head Jerk	Move head and neck backwards over back, generally while stationary.
Jump	Without a running start, jump into the air. May be accompanied by a vocalization described as barking.
Run	Move at a speed similar to or faster than an average human adult runs. Head may be held high and extended, or low and horizontal to the ground. Wings may be extended or held close to the body.
RECORDED BUT NOT ANALYZED (Behaviors were easily misidentified)	
Predator Defense Display	*Crouch with tail raised and fanned, wings loosely tucked to the body, and head and neck extended upwards.*
Tail Lift	*Lift tail up to 90° angle, with feathers fanned, and then lower tail. Often performed while sitting but can also be done while standing. Tail lifting generally occurs when another bird approaches, may be accompanied by erection of head crest feathers.*
Threat Posture	*Stand with tail up and fanned, wings outstretched, plumage ruffled and head extended forward. Wings and tail may be vibrated.*

Statistical Analysis

Statistical analysis was done in R v3.2.3. Mixed effect models were used to examine the effects of age, season, and sex on each behavior using the glmmPQL function. Year, Institution, and Individual Identity were included as random effects. A stepwise model selection using the two factors of 1) Year and 2) Individual Identity nested within Institution was run first to determine which of these factors needed to be included in the analysis. Those factors necessary to achieve the lowest AIC value were then included in the glm analysis. When the best model included no random factors, the glm function was used instead of glmmPQL. In cases where the data were institutional in nature, rather than individual, stepwise model selection included only Year and Institution.

To account for the right skew and overdispersion of the data, the models employed either a quasibinomial distribution with a logit link or a quasipoisson distribution with a log link, as appropriate for the data. We report t-statistics because the estimated regression coefficients calculated by the mixed effects models followed a Student-t distribution.

Graphing

To account for institutional differences, averages for figures were determined by first calculating an institutional average across all individuals at that institution. The figures were then produced by averaging over all institutions in each condition and calculating the standard error across institutions.

2.2 Results

Quality of Data

Recordings of Behavior

Due to the nature of the methods, with point samples being taken on birds that were not under continuous observation, as well as reliability concerns, certain behaviors from the original ethogram were combined or excluded from the analysis (see Table 2). For instance, pace and walk were combined into locomote, as these cannot be easily distinguished by point samples. Predator defense display, tail lift, and threat posture were eliminated from the analysis. After initial analysis of the first year of data collection and discussions with keepers, these behaviors were determined to be easily confused with each other and misidentified (see Table 2). All other behaviors were analyzed by “Analysis Category” as listed in Table 2.

All three maternal behaviors (see Table 2) require the opportunity to interact with eggs or chicks. Zoos differ as to whether they give females this opportunity. DZ is the only zoo that allows female kori bustards to raise their own chicks because all other zoos hand-rear the chicks. Offer food and brood chicks were therefore removed from the analysis, as only DZ females had the opportunity to perform this behavior.

All the zoos in this study, including DZ, remove eggs as soon as they are found, artificially incubating them safely away from predators. All the zoos except ZM replace the egg with a “dummy” egg (an artificial egg resembling the real egg, often made of plaster, wood), giving the female the opportunity to continue to perform the maternal behaviors of egg turning and incubating. As ZM does not replace the eggs with dummy eggs, ZM females had no opportunity to perform maternal behaviors and were removed from the analysis of maternal behaviors.

Data Set

After data cleanup, a total of 74,749 observations were used from the 50 birds at the 9 institutions in the study, for a total of 5,025 animal-weeks. Approximately 3% of data points were removed, eliminated because they were taken outside the range of 0800 to 1700 or they were recordings of eliminated behaviors as described above. On average, each animal was observed 1,705 times over 114 weeks. Each animal was observed an average of 14 times per week. Animals were observed at least 7 times in a week for 84% of the weeks.

Keepers were permitted to take extra observations beyond the scheduled three per day. This occurred in 348 weeks or 7% of the 5,025 total weeks observed. On average, extra recordings were taken on each animal in 8 weeks (7% of average 114 weeks each animal was observed). This practice varied greatly between institutions. The maximum number of observations on any animal in a week was 26 (or 5 more than the requested number of 21).

Overall Activity Budget

Overall, all the kori bustards spent most of their time resting alert (Figure 1). They also spent large amounts of time walking, performing body maintenance (e.g. preening), resting not alert, and feeding (Figure 1). Not surprisingly, there were significant differences in behavior by age, sex, and breeding season (Figure 2, see below for details). Maternal and sexual behavior are discussed in details in Section 3.

Figure 1: Overall kori bustard activity budget
Percent of observations recorded in each activity, averaged first by individual and then over all birds. Breeding behavior (maternal, sexual) are averaged for members of the appropriate sex only.

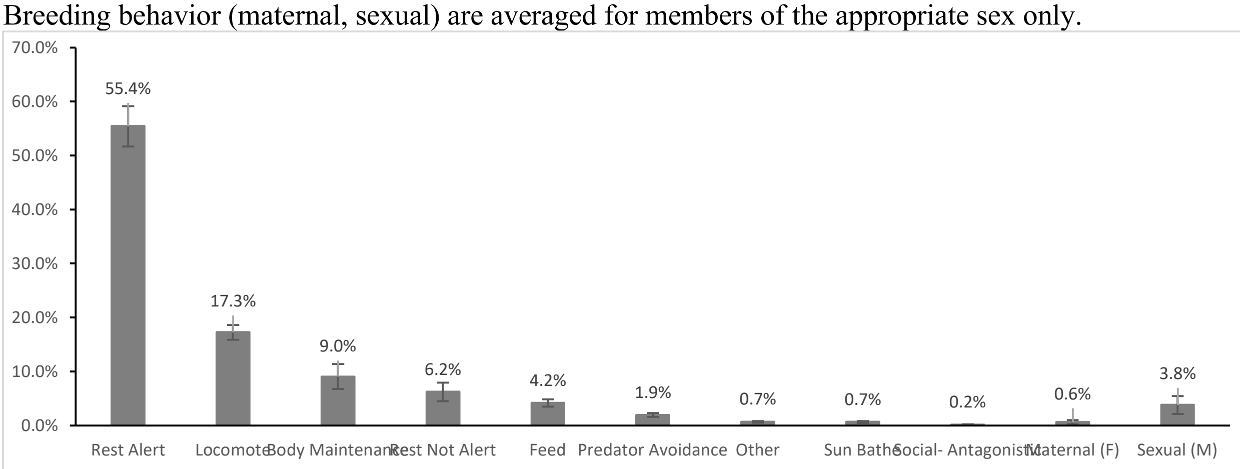
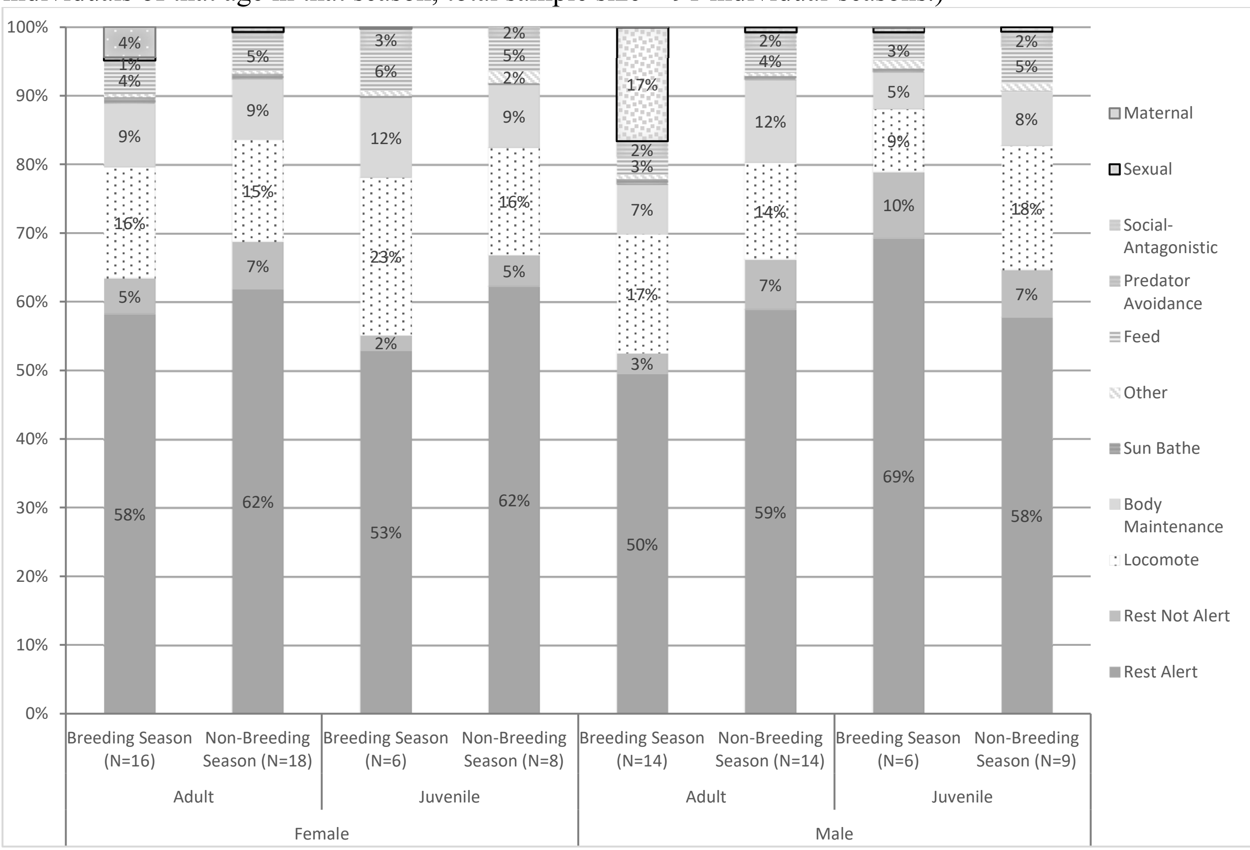


Figure 2: Activity budgets by age, sex, and breeding season
Percent of observations recorded in each activity. Unlabeled boxes represent <2% of observations. See text for description of calculations and statistics. Breeding behavior is boxed. (N represents number of individuals of that age in that season, total sample size = 91 individual-seasons.)



Age

Juveniles fed (t=2.41, p=0.02) and did predator avoidance (t=2.43, p=0.02) more than adults did. Adults, on the other hand, sunbathed more than juveniles (t=-2.13, p=0.03).

Season

During the breeding season, kori bustards rested less (alert: t=2.89, p=0.004; not alert: t= 2.94, p=0.004) and sunbathed more (t=-3.52, p=0.0005) than they did during the non-breeding season. Adult males also did less body maintenance during the breeding season than during the non-breeding season (t=2.68, p=0.008). Juveniles of both sexes performed other behaviors less during the breeding season than they did during the non-breeding season (t=2.00, p=0.05). This result was stronger in males than in females (3-way interaction effect: t=2.08, p =0.04).

Sex

Males were more likely to perform predator avoidance behaviors than females (t=2.43, p=0.02). This effect was stronger in adults than juveniles (t=-2.85, p=0.005).

3. The Impact of Social Housing on Breeding Behavior

3.1 Introduction


Photo by Lisa Barker

The desire for procreating is strong in most species, and many bird species readily breed in human care. Other species, such as flamingos (Stevens, 1991) or bustards (Johnsgard, 1991), require specific physical or social environment to entice them to reproduce. When a species does not reliably breed, the conditions that promote breeding need to be investigated using a scientific approach. This can be difficult because of small samples sizes and the inability to control influential factors. In this study, we investigate the factors that may influence the reproduction of kori bustards (*Ardeotis kori*) in human care.

An understanding of the impact of conspecifics, heterospecifics, and humans on kori bustard breeding behavior is necessary for effective management practices for kori bustards in human care. One objective of the EthoTrak study was to gain an understanding of kori bustard breeding behavior in zoos in relation to the presence of other kori bustards, to the presence of other species that share space with kori bustards, and to the presence of the public.

Conspecifics

In the wild, kori bustards have a dispersed lek breeding system in which the males display in a specific area but are up to a kilometer apart (Johnsgard, 1991; Osborne and Osborne, 1998). Though the males may not be in visual contact, they are in auditory contact. Little is known about the distance between kori bustard nests in the wild, but the average home range size of wild female kori bustards is more than 20 km^2 (Morales et. al, 2001; Osborne and Osborne, 1998). Even though the effects of conspecifics on reproductive behavior have been studied in several species (Rosenberger et al., 2020), the influences in a lekking species are not well documented (Deviche, 2014). In general, the presence of males has a positive effect on female reproductive behavior and vice-versa. Based on the breeding system of the kori bustard, we would predict that when breeding kori bustards in human care, multiple males housed at least in acoustic contact should be better for stimulating display behavior than single males (Deviche, 2014). The influence of females on each other in a lekking species is not well studied. In peahens (*Pavo cristatus*), dominant females monopolize preferred males and force subordinates to mate with unpreferred males (Petrie *et al*., 1993). Additionally, female capercaillie (*Tetrao urogallus*) housed socially interfered with conspecific nesting (Rosenberger *et al.*, 2020). Thus, housing multiple females in relatively small enclosures may increase aggressive behavior that is typically not seen in the wild because their nesting locations are dispersed, Therefore, we would predict that the presence of other females may have negative impacts on female kori bustard breeding in human care depending upon their housing situation. The analysis of conspecific housing in this study aims to investigate whether the housing arrangements of a kori bustard flock impacts breeding behavior.

Heterospecifics

The presence of other species, most noticeably various species of hoofstock and some species of birds, has been demonstrated to cause lethal and non-lethal injuries to kori bustards (Hanselmann *et al*., 2013). Current SSP guidelines therefore recommend that kori bustards not be housed with hoofstock or dangerous bird species (AZA Gruiformes TAG, 2020). Nonetheless, in some facilities, kori bustards are still housed with other bird species that have not been shown to cause increased mortality. In such cases, it is critical to know whether the presence of other species suppresses breeding behavior in the kori bustards. The aim of the analysis of heterospecific housing in this study was to investigate whether housing other species with kori bustards has an impact on the kori bustards' breeding behavior.

Humans

Understanding the effect of visitors on animals in human care is also important for assessing animal welfare, interpreting behaviors, and promoting breeding. Understanding the visitor effect may be particularly important for species such as the kori bustard, which has a low tolerance for human activity in the wild (Mmassy *et al.,* 2017) and whose breeding season in the United States generally coincides with peak crowd levels at most zoos (Hallager, 2017).

Questions

The EthoTrak data (see section 2 above) were used to answer the following questions:

1. Does male behavior affect whether females lay eggs, or how many eggs they lay?
2. Do social environmental factors, such as the presence of other kori bustards or other species, affect whether females lay eggs, or how many eggs they lay?
3. What factors impact whether a female incubates the eggs she has laid?
4. What factors influence whether males display?

3.2 Methods

For the analysis of breeding behavior, only adults were included. One zoo, PZ, had only juvenile males, and was therefore not included in this analysis. All other zoos had at least one adult male and one adult female. All adult kori bustards had physical access to members of the opposite sex.

Egg Laying Behavior

Egg laying behavior was analyzed with two measures: 1) what proportion of females at an institution laid eggs at all in a given year, and 2) how many clutches each female laid in a given year.

A clutch was considered all eggs laid within four days of each other. This was determined based on egg logs collected at each zoo. Egg logs recorded the date each egg was laid, the dam, the sire if known, and the outcome (infertile, hatched, etc.). The number of clutches was used instead of the number of eggs because the total number of eggs can be difficult to determine and has been found not to be a consistently accurate measure (S. Hallager, personal observation, 2018).

Female #131 at DZ was allowed to raise chicks in the summers of 2007, 2008, and 2009. Because of this, she laid fewer eggs during those summers than she did during the summers when she did not raise chicks (Table 3). Her clutches from those years were therefore removed from the analysis of the number of clutches laid per female.

Table 3. Clutches laid per year by females at DZ. Female #131 laid fewer clutches in the years she raised chicks (2007-2009) than in the other years (2010-2012). As none of the other females showed a similar increase, this was more likely due to raising chicks than to a change in management practices.

Year	#131	#57	#136	#623
2007	3	4	3	
2008	3	4	4	
2009	3	4	5	
2010	**6**	**4**		
2011	**5**	**2**		**3**
2012	**0**	**6**		**5**

Maternal Behavior

Maternal behavior was analyzed as the rate of egg turning and incubation during the seven days after the first egg of the clutch was laid. As some species wait until the last egg of a clutch is laid before beginning incubation, we first confirmed that the birds were beginning their incubation when the first egg was laid. We observed 40 clutches with two eggs and one with three eggs. The average time between eggs was two days. Twenty-two (55%) of these nests showed incubation on the day the first egg was laid and 27 (68%) in the first two days. It was therefore determined that kori bustards do not wait for the entire clutch to be laid and maternal behavior was evaluated for the seven days after the first egg was laid.

As described above (see Section 2: EthoTrak Study), all zoos except ZM gave their females dummy eggs to incubate after removing the eggs to be incubated. ZM was therefore removed from the analysis of maternal behavior.

Male Sexual Behavior

Male sexual behavior was analyzed as the rate of sexual behavior (see Table 2) as a proportion of total behavior. Before deciding to use all males for the analysis of female behavior, it was confirmed that dominant males were not inhibiting the display behavior of other males (see Results).

Other Factors

The impact of several other factors on kori bustard breeding behavior were investigated (Table 4).

Table 4. Factors by zoo. Total N=32 zoo-years.

Institution	Years Observed	F-F Contact	M-M Contact	On/Off Exhibit	Other Species
BZ	5	Alone	Alone	Off	No
CMZ	2	Alone	Acoustic	Both*	Yes
DZ	6	Visual	Visual	Off	Yes and No†
LDZ	6	Alone	Alone	Both*	No
SNZP	6	Physical	Alone (3 yr) Acoustic (3 yr)	On	No
WOCC	3	Alone	Alone	Off	No
ZA	1	Alone	Alone	On	No
ZM	3	Visual	Visual	Off	No

*Individuals at CMZ were in both on- and off-exhibit enclosures during each year. At LDZ, some individuals were kept in an on-exhibit enclosure and others in an off-exhibit enclosure.

†DZ had one enclosure (the Scrub) that had other bird species. DZ's other enclosures did not. Most individual kori bustards were in the Scrub enclosure some of the time.

The Presence of Other Kori Bustards

All adult kori bustards had physical access to members of the opposite sex but the amount of access to members of the same sex varied. The enclosures were divided into four categories of access to conspecifics of the same sex: physical (sharing an enclosure), visual (able to see and hear another kori bustard of the same sex but with no physical contact), acoustic (able to hear another kori bustard of the same sex but not see it), and alone (not able to hear or see any kori bustards of the same sex. Because of documented aggression issues (Hallager personal observation 2020), no males were in physical contact with other males. One male was in acoustic contact only with a juvenile male. No females were in solely acoustic visual contact with other females, i.e. if a female could hear another female, then she could also see her.

The Presence of Other Species

Two enclosures in our study housed kori bustards with other species:

- DZ Scrub exhibit – two species of birds (Egyptian vulture *Neophron percnopterus* and hooded vulture *Necrosyrtes monachus*)
- CMZ – five species of birds (helmeted guineafowl *Numida meleagris*, vulturine guineafowl *Acryllium vulturinum*, cattle egret *Bubulcus ibis*, Cape vulture *Gyps coprotheres,* and griffon vulture *G. fulvus*)

No eggs were laid in either of these enclosures. This measure was therefore only used to analyze the impact on male display behavior.

The Presence of the Public

Recordings were made in 21 holding areas: 19 outdoor enclosures and 2 inside barns. The number of spaces at each zoo varied from one to five, averaging 2.3 spaces/zoo. Some of these spaces were in use at different times during the data collection (BZ, LDZ), some were used primarily by different individuals (ZM, SNZP), and others were used by different individuals at different times (CMZ, DZ). Outdoor enclosures varied with types of plantings but generally contained mature deciduous and non-deciduous trees, small ornamental grass clumps, and grass, sand or dirt.

Of the 19 outdoor enclosures, 7 were "on" exhibit and 12 were "off" exhibit. On-exhibit enclosures had at least one fence-line where the public could stand and look at the birds. Off-exhibit enclosures were only accessible to staff. Birds in both types of enclosure encountered humans but birds in off-exhibit enclosures encountered far fewer humans, and most of the humans were familiar to the birds.

For each EthoTrak observation, crowd sizes at on-exhibit enclosures were estimated as none, low, medium, or high. Observations where crowd size was left blank were eliminated from the analysis of crowd size, under the assumption that the observer forgot to record the crowd size. Observations where crowd size was listed as "N/A" for an on-exhibit enclosure (an option meant for the off-exhibit enclosures) were changed to "none." This was under the assumption that the observer considered no crowd possible, e.g.

because the zoo was closed, but that the birds would not know the difference between no crowd and no crowd possible.

To determine the average crowd size, the proportion of observations in each condition (listed below as P_{none}, P_{low}, P_{med}, P_{high}) was determined for the appropriate time period. The average number of people in a crowd for each condition were estimated as 0 for none, 5 for low, 15 for medium, and 25 for high. The average crowd was determined as follows:

$$\text{Av Crowd} = 0^* P_{none} + 5^* P_{low} + 15^* P_{med} + 25^* P_{high}.$$

Statistical Analysis and Graphing

Statistical analysis was done in R v3.2.3 in the same way as the Activity Budget analysis (see section 2.1). Mixed effect models were used to separately examine the effects on each variable of male sexual behavior, institution, access to same-sex conspecifics, whether the birds were on or off exhibit, the presence of other species, and crowd size. Year, Institution, and Individual Identity were again included as random effects. As above, we report t-statistics because the estimated regression coefficients calculated by the mixed effects models followed a Student-t distribution.

As before, averages for figures were determined by first calculating an institutional average across all individuals at that institution. The figures were then produced by averaging over all institutions in each condition and calculating the standard error across institutions.

3.3 Results

3.3.1 Total Clutches

A total of 78 clutches were laid by 10 females at four zoos (BZ, DZ, SNZP, and ZM). An average of 57 ±9% of the females at these zoos laid eggs. Females at these zoos laid an average of 1.6 ±0.3 clutches per year. Four zoos (CMZ, LDZ, WOCC, and ZA) had no eggs laid. Overall, 56% (10/18) of the females bred, at 50% (4/8) of the zoos.

3.3.2 Does Male Sexual Behavior Affect Female Egg-Laying Behavior?

Will females lay at all without males?

The first question in whether male breeding behavior impacts female breeding behavior is whether females will lay eggs if no displaying males are present. Zoos were characterized as to whether any males displayed and any females laid. There were zoos where no males displayed and no females laid. Although there were zoos in which males displayed but females did not lay, there were no zoos in which females laid but males did not display (Table 5).

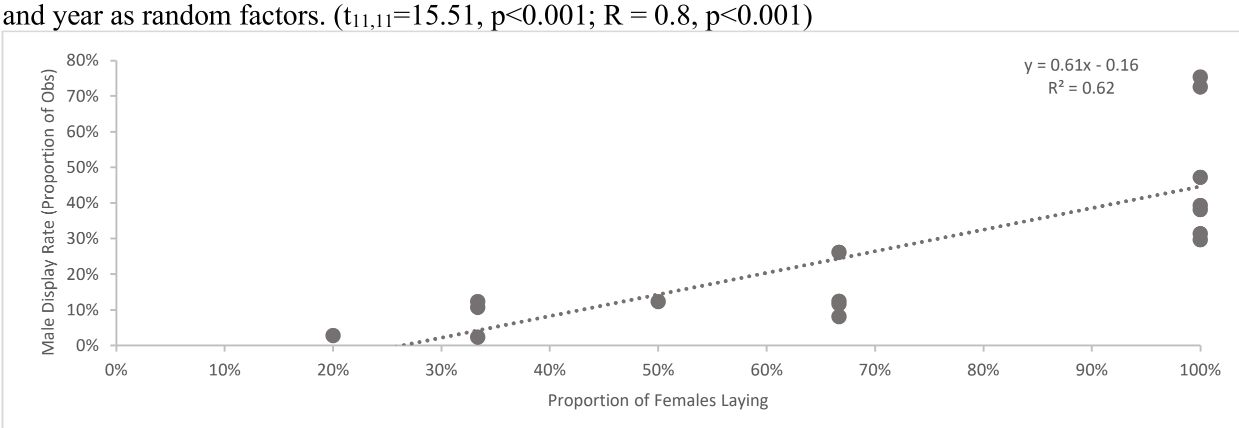
Table 5. Zoo-years where males performed sexual behavior vs zoo-years where females laid eggs. N = 32 zoo-years.

	No Females Laid	At least 1 Female Laid
No Males Displayed	**10**	**0**
At least 1 Male Displayed	**6**	**16**

Proportion of females laying

The proportion of females laying eggs was directly and significantly related to the amount of sexual behavior showed by the males (Figure 3, correlation coefficient = 0.8, $p<0.001$, glm: $t_{11,11}=15.51$, $p<0.001$). The more the males displayed, the more of the females that laid eggs. For this analysis, male sexual behavior was averaged over all males at each institution for each year, from the first recording of sexual behavior to the date the last clutch was laid *at that institution* in that year.

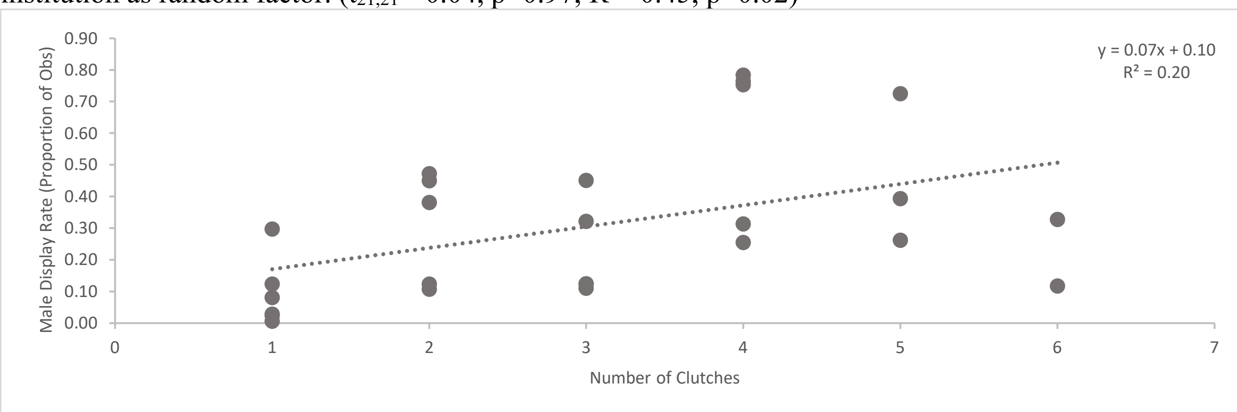
Figure 3. The proportion of females laying by the proportion of time males at that institution spent displaying. Analysis: general linear mixed models, quasibinomial distribution with a logit link, institution and year as random factors. ($t_{11,11}=15.51$, $p<0.001$; R = 0.8, $p<0.001$)



Number of clutches per female

The number of clutches per female was only weakly correlated with the amount of sexual behavior to which the females were exposed and not significantly related by the mixed models (Figure 4, correlation coefficient = 0.45, p=0.02, glm: $t_{21,21}$=-0.04, p=0.97). For this analysis, male display behavior was averaged over all males at each institution for each year, from the first recording of sexual behavior to the date the last clutch was laid *by that female* in that year.

Figure 4. The number of clutches laid per females by the proportion of time males at that institution spent displaying. Analysis: general linear mixed models, quasipoisson distribution with a log link, institution as random factor. ($t_{21,21}$=-0.04, p=0.97; R = 0.45, p=0.02)



Summary

The amount of male sexual behavior was a primary factor in whether the females laid eggs but only one of many factors in how many clutches a given female laid. We tested to see whether the crucial factor was the amount of male sexual behavior or the number of males displaying. However, our variation was low (BZ and SNZP had 1 male, DZ and ZM had 2 males). What variation we had did not impact laying behavior in any way.

3.3.3 Do Environmental and/or Social Factors Affect Female Egg-Laying Behavior?

Institutional effects

The strongest impact on female laying behavior came from the institution, with DZ having a greater proportion of females laying and more clutches than any other zoo (Table 6, Figure 5, Appendix A.1). The difference in the proportion of females laying was not quite significant (p=0.09), partly because the year-to-year variation at BZ and ZM was very high. However, the difference in number of clutches was significant, with DZ females producing an average of four clutches per year, compared to females at other zoos producing no more than one on average (p=0.01). This institutional effect overshadowed many of the other factors we tested.

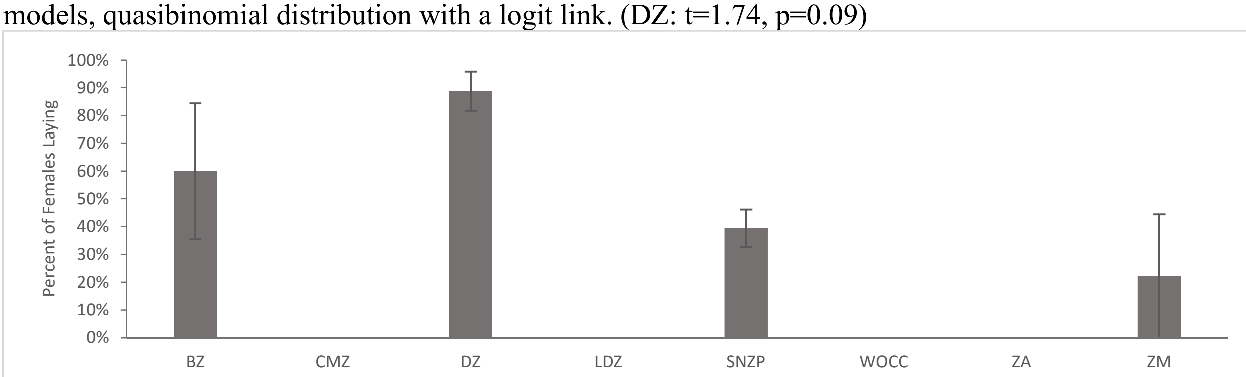
Table 6. Female kori bustard laying behavior by zoo per year.

Institution	Proportion of Females Laying*		Clutches per Female *for females who laid only*†	
	Average	P-value (to BZ)	**Average**	P-value (to BZ)
DZ	89% ±7%	0.09	**4.3 ±0.3**	**0.02** (t=3.23)
BZ	60% ±24%	N/A	1.7 ±0.3	N/A
SNZP	39% ±7%	0.28	1.8 ±0.3	0.88
ZM	22% ±22%	0.11	2.0	0.68
CMZ	0%	1		
LDZ	0%	1		
WOCC	0%	1		
ZA	0%	1		

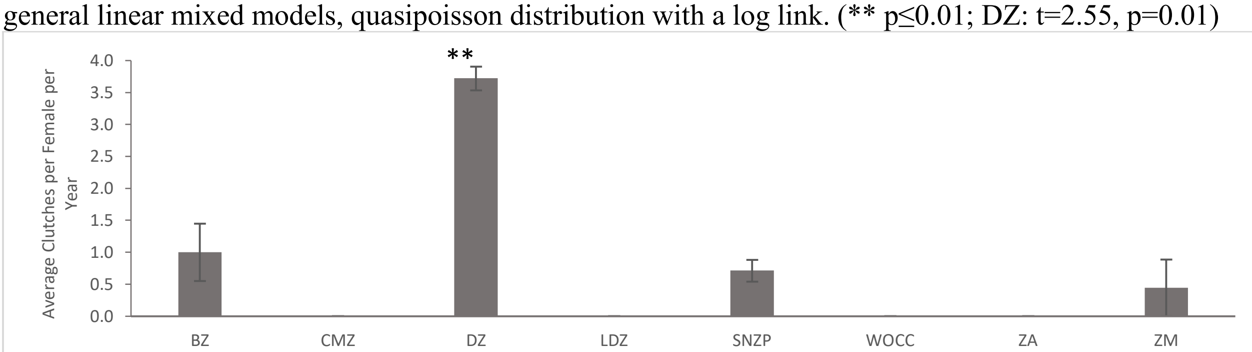
*N = 32 zoo-years with 18 females
†N = 78 clutches in 16 zoo-years with 10 females

Figure 5. Institutional Differences in Female Behavior

5a: Average percent of females at each institution laying per year. Analysis: general linear mixed models, quasibinomial distribution with a logit link. (DZ: t=1.74, p=0.09)



5b: Average clutches per female per year (for all females, including those that did not lay)**.** Analysis: general linear mixed models, quasipoisson distribution with a log link. (** p≤0.01; DZ: t=2.55, p=0.01)



Female-female contact

There was a slight but non-significant trend toward females with visual contact to other females being more likely to lay and laying more clutches (glm: p=0.14 and p=0.10). However, this was primarily driven by DZ, where females were in visual contact (see Figure 5, Appendix A.2).

On vs off exhibit

There was a slight but non-significant trend toward females laying more when off exhibit (glm: p=0.46 and p=0.40). Again, with all of DZ females off exhibit, this result could not be distinguished from the institutional differences (see Appendix A.3). Only one zoo, CMZ, had both enclosures that were on-exhibit and enclosures that were off-exhibit. As no eggs were laid at CMZ, there was no difference between including CMZ in both the on and off categories or excluding it. CMZ was therefore excluded from this analysis.

Crowd size

The impact of crowd size could be distinguished from institutional differences, however, as DZ with its off-exhibit enclosures was not included in this analysis. Four zoos kept their kori bustards on-exhibit during this study: CMZ, LDZ, SNZP, and ZA. Of these, only SNZP had eggs laid. SNZP also had the highest crowd sizes of these four institutions, indicating that the presence of a crowd does not inhibit egg laying. Because only SNZP had eggs laid, only SNZP is included in the following analysis.

For analysis of the *proportion of females laying*, crowd was averaged over all observations at the institution for each year, from one week before the first clutch was laid to the date the last clutch was laid *at that institution* in that year. For analysis of the *number of clutches per female*, crowd was averaged over all observations at the institution for each year, from one week before the first clutch was laid to the date the last clutch was laid *by that female* in that year.

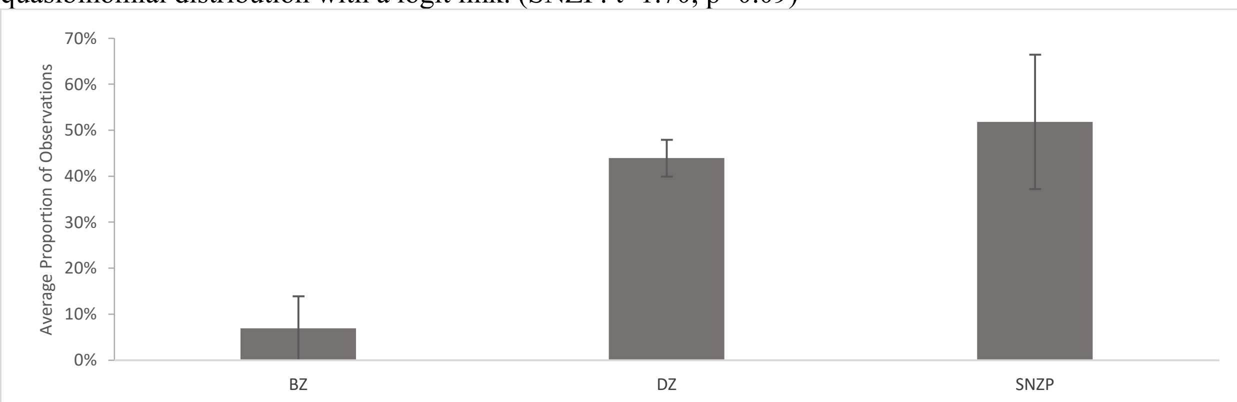
Crowds had no significant impact on either the proportion of females laying or the number of clutches per female per year (see Appendix A.4). The proportion of females laying was negatively correlated to the average crowd size, but this correlation was not significant (R=-0.6, p=0.24). The number of clutches laid per female was not correlated with crowd size (R=-0.1, p=0.77).

3.3.4 What Factors Impact Maternal Behavior?

Institutional effects

On average, females with eggs spent 43 ±4% of the week after laying incubating those eggs. This varied considerably by institution, with the BZ female showing an unusually low amount of maternal behavior (Figure 6, Appendix A.5). That difference was not quite statistically significant, however (P=0.09). As each of the three institutions had different female-to-female access, the impact of female access could not be distinguished from institutional differences (see Table 4).

Figure 6: Average time spent incubating in the week after a clutch was laid. ZM is not included because they removed the eggs without replacing them with dummy eggs. Analysis: general linear mixed models, quasibinomial distribution with a logit link. (SNZP: t=1.70, p=0.09)



Other effects

There was no significant impact of whether the eggs were laid on- or off-exhibit, or of crowd size, on maternal behavior (P=0.5 for on/off, P>0.9 for all crowd sizes). Of the four on-exhibit zoos, only SNZP had any eggs laid, and therefore only SNZP was included in the analysis of crowd impact on maternal behavior. For this analysis, behavior was compared in the four different crowd conditions.

Similarly, males displaying had no impact on maternal behavior (P=0.4 for males' behavior the week before the clutch was laid, and P=0.1 for the week the clutch was laid). For this analysis, male sexual behavior was averaged over all males at the institution in two ways: 1) for the week before the clutch was laid, and 2) for the week after the clutch was laid.

3.3.5 What Factors Influence Male Sexual Behavior?

Photo by Meghan Murphy

For this analysis, male sexual behavior was determined for each male for the entire year. 79% (11/14) of the males, at seven of the eight zoos, displayed sexual behavior in at least one year. Males were observed in an average of 3 ±0.4 years. Males that displayed sexual behavior did so in 82 ±8% of the years that they were observed. The majority of these males (7/11 = 64%) displayed every year they were observed.

Dominance

Our first question was whether dominant males were interfering with display behavior by subordinate males. In other words, do institutions with multiple males have a single male who displayed or did all their males display? To investigate this, we looked at the proportion of males displaying by whether they could see or hear other males, i.e. whether they had visual or acoustic access to other males. If only a dominant male displays, i.e. the males are interfering with each other, we would expect institutions where males had visual and/or acoustic access to each other to have a lower percentage of males displaying. In other words, the likelihood of males displaying when they were alone, as measured by the average number of males alone at institutions in our study who displayed, should be higher than the average number of males who displayed at institutions with multiple males. This did not turn out to be the case (Table 7). In fact, institutions where males had visual and/or acoustic access to each other had a higher percentage of males displaying, although this difference was not significant. This may suggest that multiple males actually stimulate each other to display.

Table 7. Percent of males displaying by access to other males.
Total N = 31 zoo-years

Access	Percent Males Displaying	N	P-value
None (Alone)	**59%** ±12%	17	
Acoustic	**60%** ±19%	5	0.99
Visual & Acoustic	**93%** ± 5%	9	0.13

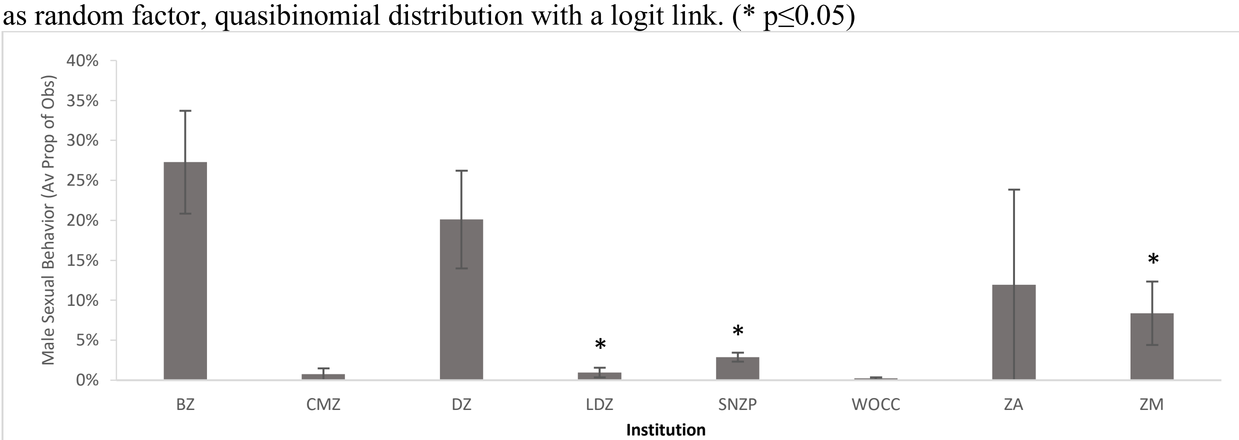
Institutional and environmental effects

On average, males spent 10 ±2% of their time displaying over the year. This varied significantly by institution (Figure 7a). Institutional factors played some part in this (Figure 7b). The clearest impact was that males in exhibits with other species of birds performed significantly fewer display behaviors than males in kori-only exhibits ($t_{42,42}$=2.11, P=0.04). In addition, males performed slightly but not significantly more sexual behaviors when off-exhibit than when on-exhibit (P=0.09). Males with visual access to other males performed more display behaviors, and males with only acoustic access performed fewer, but neither difference was significant (Figure 7c; Visual: $t_{36,6}$=1.55, P=0.2; Acoustic, $t_{36,36}$=-1.07, P=0.3).

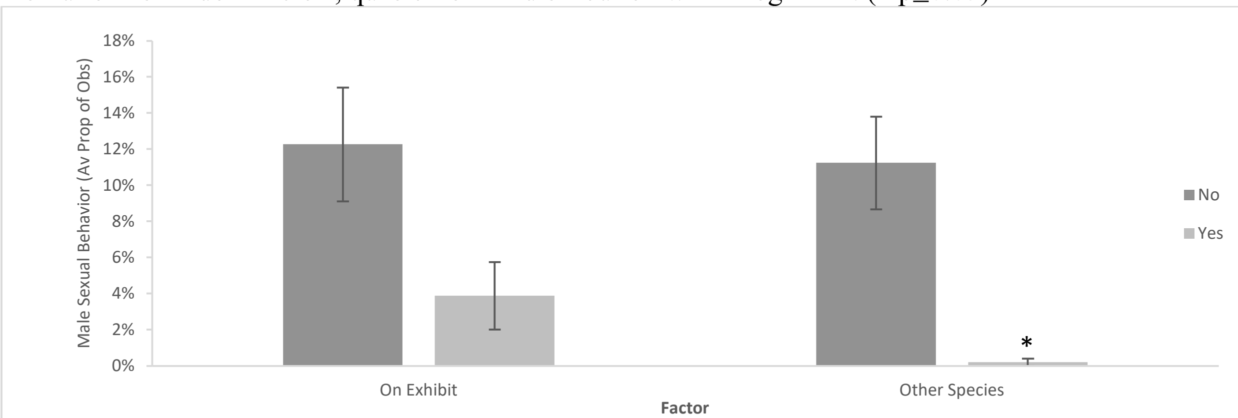
Crowds was positively related to male display behavior (Figure 7d). Males displayed significantly more often with medium or high crowds than with low or no crowds (none: $t_{43,43}$=-3.5, p=0.001; Low: $t_{43,43}$=-2.6, p=0.01). For this analysis, behavior was compared in the four different crowd conditions.

Figure 7. Male Sexual Behavior

7a: Institutional differences in male display behavior. Analysis: general linear mixed models, individual as random factor, quasibinomial distribution with a logit link. (* p≤0.05)

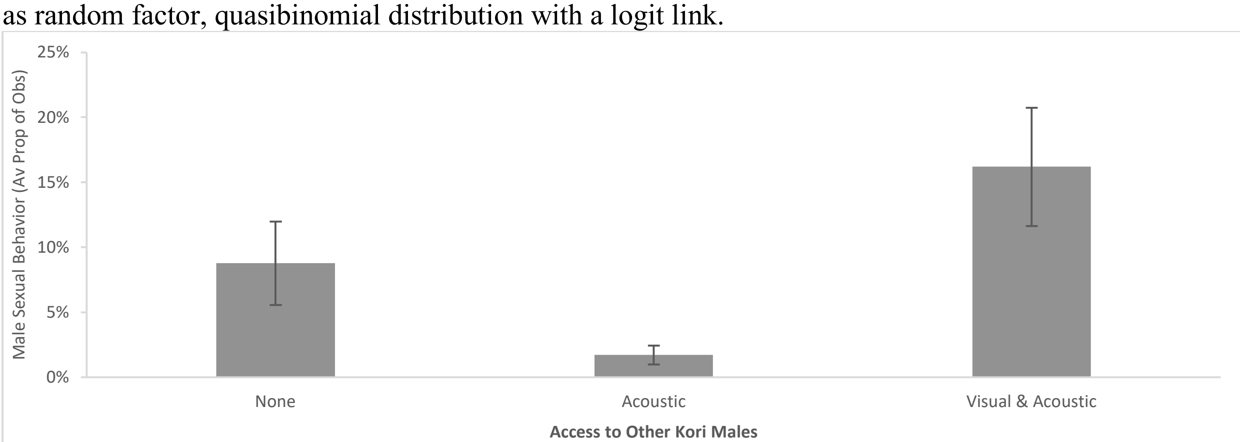


7b: Management Factors influencing male display behavior. Analysis: general linear mixed models, institution as random factor†, quasibinomial distribution with a logit link. (* p≤0.05)

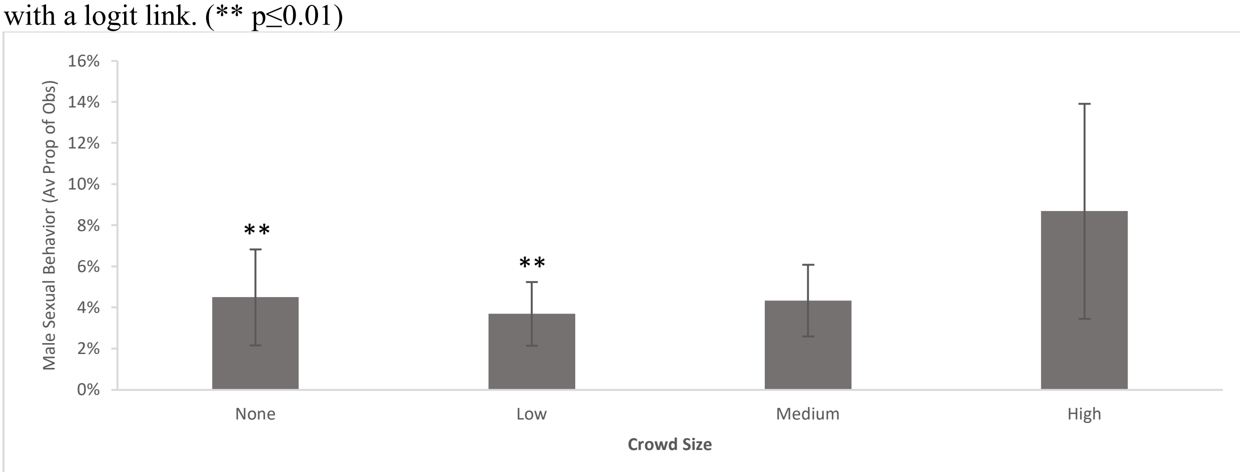


†For On Exhibit, random factors were institution and year.

7c: Social Factors influencing male display behavior. Analysis: general linear mixed models, institution as random factor, quasibinomial distribution with a logit link.



7d: The impact of crowd size on male display behavior, for on-exhibit enclosures only. Analysis: general linear mixed models, individual nested in institution as random factor, quasibinomial distribution with a logit link. (** p≤0.01)



3.4 Discussion

Impact of Kori Bustards on Each Other

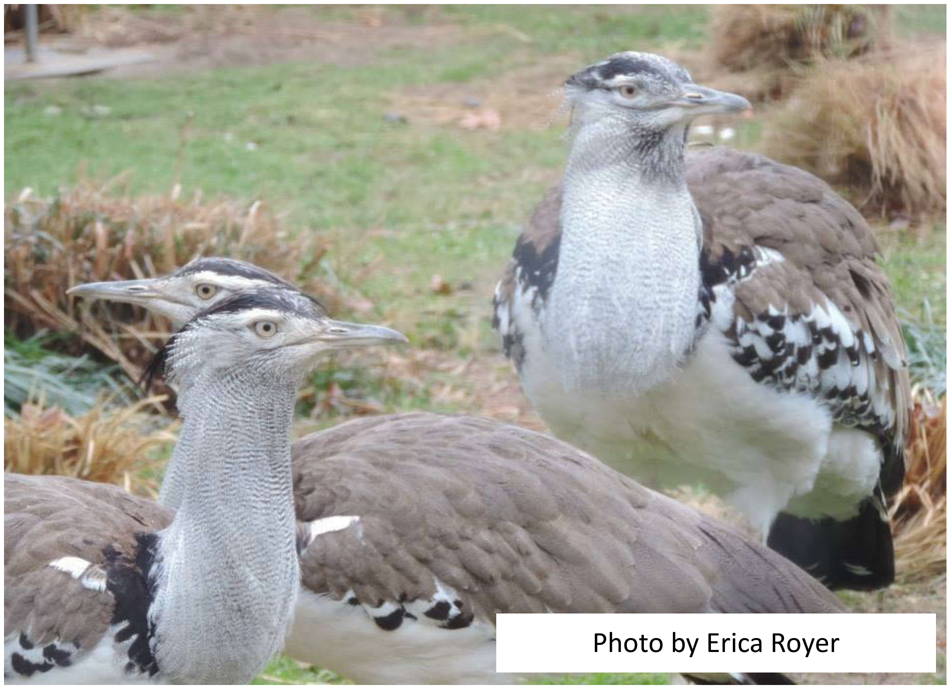


Photo by Erica Royer

In a lekking species, male display behavior is expected to have an impact on the breeding behavior of other individuals (Morales, *et al.*, 2001). In the current study, males were somewhat more likely to display at institutions with multiple males, suggesting that males may have been stimulating each other to display. This supports our prediction for kori bustards, which have an exploded lek display where males display in an assemblage spread out over a large area (Bradbury, 1981). This suggests that an *ex-situ* population with multiple males will achieve better reproductive success. In the current study, this result was a trend but was not significant, indicating that more study is needed. Whether male kori bustards in human care follow similar behavioral display patterns as their wild counterparts needs further study especially given anecdotal observations by keepers in the early 1990s describing subordinate males being inhibited by dominate males (Hallager and Boylan, 2004).

Male sexual display behavior also impacted female breeding behavior, in that females only laid eggs at institutions with displaying males. In fact, the proportion of females laying at an institution was correlated with the amount that males displayed. This may indicate that male sexual behavior is stimulating female egg laying. An institution with multiple females but only one male might therefore have difficulty getting all of their females to lay. As kori bustards in the wild use a dispersed lek (Johnsgard, 1991; Osborne and Osborne, 1998), females in the wild can be expected to hear more males displaying than they see. Music has been employed in field studies to attract songbirds (Hurd, 1966), as well as in language studies with African grey parrots (Pepperberg, 1981). Pet bird owners regularly play music for their birds (King, 1993). Bird and Johnson (2001) suggested that the playback of calls could be used to stimulate breeding and territorial calls. It would be worth investigating whether playing the sounds of displaying males in the vicinity of females is sufficient to stimulate egg laying in kori bustards under human care.

Impact of Other Birds on Koris

Heterospecific exhibit-mates are a known concern for kori bustards with sometimes lethal consequences (Hanselmann *et al*., 2013). We found that heterospecific exhibit-mates can also have non-lethal affects by influencing the behavior of kori bustards. In our study, various species of birds housed with kori bustards affected male breeding behavior. Adult male kori bustards in the two exhibits with heterospecific birds displayed fewer sexual behaviors than the males in exhibits without heterospecific birds. With the small number of exhibits, it is difficult to tell whether other factors may be at play, for example individual male temperament, management techniques, size of enclosure, etc. In smaller enclosures, the influence of other species may be greater. The San Diego Zoo Wild Animal Park has successfully bred kori bustards in a multi-species exhibit that is approximately 700 m^2 (7500 ft^2). These results, however, reinforce the recommendation that managers should exercise caution when housing kori bustards with other species. Future studies in this area of research that could tease apart the influence of heterospecifics, exhibit size, and management techniques would be very beneficial.

Impact of Humans on Kori Bustards

Kori bustards are often considered nervous birds especially in the presence of humans (S. Hallager, personal observation, 2020), and as such, their behavior might be expected to be disrupted by large crowds. There were some indications that both males and females performed more breeding behavior, and laid more eggs, off-exhibit than on-exhibit. This effect was overwhelmed by the unusually successful breeding at DZ, however, and therefore needs additional study.

However, in the current study, crowds did not disrupt breeding behavior in either males or females. In fact, there was some indication that males displayed more at higher crowd levels. Although it is possible that the crowds are stimulating male display behavior, it is more likely that they are merely correlated. The trend toward increased breeding behavior off-exhibit suggests this as well. One likely correlate is the weather. Kori breeding seasons in the US occur in the spring and summer months, when the weather is nicest. Crowds tend to be higher on nice days (Perkins, 2012).

Institutional Impacts

DZ had an unusually large number of eggs laid, which overwhelmed our ability to distinguish the impact of specific institutional factors. DZ's combination of factors was not unique: ZM had the same combination of both males and females in visual contact with same-sex conspecifics, most birds in kori-only exhibits, and off-exhibit enclosures. Nor did DZ have a larger number of birds (DZ: 3 males, 4 females; ZM: 3 males, 3 females). However, DZ had significantly more eggs laid than ZM. This suggests that factors are at play that have not been considered in the current study or possibly because ZM's flock was fairly new and may not have yet acclimated (Penfold *et al*., 2013). Further study of environmental or management factors may shed some light on this disparity.

4. Hand and Parent Rearing of Kori Bustard Chicks Lead to Equivalent Outcomes

4.1 Introduction

Rearing methods of animals under human care vary, with the most common being parent-rearing and hand-rearing. Some animals are reared for the sole purpose of reintroduction and rearing conditions therefore must be carefully considered as they will affect their future survival, reproduction, and social interactions (Hutchins *et al*., 1995; Kleiman *et al*., 1991; Snyder *et al*., 1996; van Heezik and Seddon, 1998). Among bustards, those reared for release include houbara bustard (*Chlamydotis undulata*) of which (*C.u.undulata*) is hand-reared and reintroduced for hunting and (*C.u.macqueenii*) is hand-reared for restoration of wild populations (van Heezik and Seddon, 1998). Great bustards (*Otis tarda*) are hand-reared for reintroduction to the United Kingdom (Great Bustard Group Member Update June 2020) and recently, great Indian bustard (*Ardeotis nigriceps*) are being reared as insurance populations against extinction (Jhala, *et al*., 2020).

Photo by Jessie Cohen

Some bustard species, however, are reared solely for the purposes of maintaining sustainable *ex situ* populations (e.g. white-bellied bustard *Eupodotis senegalensis* (Species360, 2017; zims.Species360.org), buff-crested bustard *Lophotis gindiana* (Hallager and Ballou, 2015b), black bustard *Eupodotis afra* (Gregson, 1986), and kori bustard *Ardeotis kori* (Hallager, 2017)).

Survival, reproduction, and social interactions are just as important for birds in human care as they are for birds destined for the wild. An understanding of chick development and behavior, and the implications of these to future reproduction is critical to any successful *ex situ* breeding program. For poorly understood species such as bustards, it is especially critical as less than half of the world's 25 species of bustards have been propagated in human care, and their needs under human care are not fully understood. As bustard populations decline worldwide, gaining a better understanding of bustard husbandry is vital to any future propagation program.

Since 1993, a breeding program for the kori bustard in the United States has been managed under the auspices of the Association of Zoos and Aquariums as a Species Survival Plan (SSP®). The kori bustard SSP program has no plans to reintroduce birds as the wild population is not currently in need of birds. Since 1992, 190 chicks have hatched in 15 facilities within the United States (Hallager, 2016). Nearly all chicks in the United States (>80%) have been hand-reared, with only one facility parent-rearing offspring. The choice to hand-rear has been intentional. Managers desired birds that were acclimated to humans, given perceptions that kori bustards were generally nervous, accident prone, and avoided close proximity to humans (S. Hallager, personal observation, 2017).

To create a self-sustaining population, it is important that chicks are raised in a way that produces birds that survive to adulthood, are behaviorally normal, and can successfully breed. We therefore investigated the impacts of the choice to hand- or parent-rear kori bustard chicks, and whether both strategies are equally successful at raising birds that are successful breeders.

Questions

The EthoTrak data, combined with studbook data and data on hand-reared chick behavior, were used to address the following questions:

- Do hand-reared (HR) and parent-reared (PR) chicks survive to adulthood at similar rates?
- Do HR and PR chicks have equivalent behavior as chicks and as adults?
- Do the chicks hatched from HR and PR adults survive to adulthood at equivalent rates, and do they survive at equivalent rates to the chicks hatched from wild-caught (WC) birds?

4.2 Chick Survival

Methods

The survival of chicks hatched since 1992 was determined based on a search of the 2016 studbook (Hallager, 2016) performed on 21 May 2016. "Adulthood" was designated as three years, the youngest age at which kori bustards have been documented breeding in human care (Hallager, 2016). Chicks younger than three years at the time of the search were excluded from the dataset. The dataset therefore only includes birds hatched between 1992 and 2012.

The dataset included parent-reared chicks from three dams at Dallas Zoo and hand-reared chicks from 14 AZA-accredited institutions (Audubon Zoo, Birmingham Zoo, Cameron Park Zoo, Dallas Zoo, Franklin Park Zoo, Jacksonville Zoo and Gardens, San Diego Zoo Safari Park, Sedgwick County Zoo, Smithsonian National Zoological Park, St. Catherine's Island / Wildlife Conservancy Society, Phoenix Zoo, Toledo Zoological Gardens, Zoo Atlanta, and Zoo Miami). Because the dataset included unequal samples sizes between institutions and between dams, we calculated percent survival by first averaging by institution for HR birds and by dam for PR birds. Differences in HR vs PR were tested by non-parametric Kruskal-Wallis tests.

Data Set

Between 1992 and 2012, 151 kori bustards hatched at SSP zoos: 126 HR, 25 PR. Overall, 50% (75/151) of these chicks survived to be adults.

Results

Hand-rearing and parent-rearing of kori bustards were equally successful at producing chicks that survived to adulthood (Table 8). Chick survival did not differ by type of rearing (H_1=0.58, P=0.81). Overall, 50% (63/126) of HR chicks and 48% (12/25) of PR chicks survived (Table 9). When averaged by who actually raised the chicks, 40 ± 8% of HR and 45 ± 5% of PR chicks survived (Tables 8, 9).

Table 8: Survival of Chicks to Adulthood (3 years) by Type of Rearing

Sex	Rearing	Percent Survival	Averaged % Survival*	KW-test P-value (stat)
Total†	Hand	50% (63/126)	40% ± 8%	0.81 (H_1=0.58)
	Parent	48% (12/25)	45% ± 5%	
Female	Hand	60% (28/47)	58% ± 13%	0.54 (H_1=0.38)
	Parent	63% (5/8)	79% ± 21%	
Male	Hand	60% (35/58)	47% ± 12%	0.71 (H_1=0142)
	Parent	67% (6/9)	61% ± 11%	

*Averaged by who actually raised the chicks – by institution for hand-reared birds and by dam for parent-reared birds.
†Includes 29 chicks of unknown sex. All but one of these died before reaching adulthood.

Of the chicks, 122 were of known sex (67 male, 55 female). Overall, 66% (44/67) of the males survived compared to 60% (33/55) of the females. When the bias of unequal sample sizes was removed by averaging by institution for HR birds and by dam for PR birds, 49 ± 10% of the males and 61 ± 11% of the females survived. There was no difference in survival between males and females (H_1=0.85, P=0.36).

To determine whether there was any interaction between chick sex and type of rearing in chick survival rates, the impact of type of rearing was also investigated separately for known males and females (Table 8). There were no significant differences in survival by type of rearing for either males or females.

Table 9: Survival of Chicks to Adulthood (3 years) by Who Raised Them

Rearing	Who Raised: Location/Dam	Total Hatches	% Survive to Adulthood
Hand-Raised	Zoo 1	5	20% (1)
	Zoo 2	1	0% (0)
	Zoo 3	4	25% (1)
	Zoo 4	2	48% (1)
	Zoo 5	2	50% (1)
	Zoo 6	6	33% (2)
	Zoo 7	34	35% (12)
	Zoo 8	9	56% (5)
	Zoo 9	1	0% (0)
	Zoo 10	52	65% (34)
	Zoo 11	2	0% (0)
	Zoo 12	2	50% (1)
	Zoo 13	2	100% (2)
	Zoo 14	4	75% (3)
	Total Hand-Raised	***126***	***50%* (63)***
Parent-Reared	Dam 1	5	40% (2)
	Dam 2	20	50% (10)
	Total Parent-Reared	***25***	***48%* (12)***

*Overall percent survival, not averaged by location or dam.

4.3 Chick Behavior

Methods

Behavioral data from HR chicks in weeks 1 to 8 at the Smithsonian National Zoological Park (SNZP) were compared to data from dam-reared (PR) chicks of the same age at Dallas Zoo (DZ). The behavior of HR chicks was collected at SNZP between 2008 and 2015. Friends of the National Zoo volunteer kori bustard behavior watchers took observational data on the chicks between 8:00 and 16:00, for one hour at a time, for a total of 446 hours across 290 days in 8 years (no chicks were hatched in 2014). During the hour, scans were taken every 5 minutes (Table 10). All occurrences of additional behaviors were recorded continuously but are not analyzed here, as they were rare. The behavior of PR chicks at DZ was collected as part of the larger EthoTrak study (see Table 2 in Section 2 & Table 10 below). As the EthoTrak data collection did not record when a chick was not visible, "not visible" recordings from the SNZP data were discounted. Data therefore represent the percent of time visible. As in the Activity Budget analysis in

Section 2, pace and walk were combined into locomote, as these cannot be easily distinguished by point samples.

Table 10. Ethogram of Scan Behaviors used in the SNZP chick study.

Behavior	EthoTrak Equivalent	Description
Alert	Rest Alert	Stationary (sitting or standing) with neck extended (maintaining an alert status)
Forage/Feed		
Feed	Feed	Peck at food within reach or chase down jumping or flying prey
Forage		Search for food while walking (looking down)
Keeper Feed	Chick Feed	Keeper in enclosure, feeding the chicks (DZ: dam feeding chicks)
Locomote		
Pace	Pace	Walk back and forth in a particular area at a quickened pace
Walk	Walk	Move throughout enclosure at a leisurely pace
Preen	Body Maintenance	Use bill to straighten feathers on breast, neck, tail, legs, or wings (sitting or standing)
Run	Run	Move rapidly through the exhibit (often to escape a perceived threat)
Rest	Rest Not Alert	Stationary (sitting or standing) with neck tucked back
Sun	Sunbathe	Sit with one or both wings spread horizontally
Not Visible	(None)*	Chick is not visible

*The EthoTrak data did not record when chicks were not visible, so these recordings from SNZP were discounted. Data therefore represent the percent of time visible.

The proportion of time spent in each of the SNZP scan behaviors, or the EthoTrak equivalents for the DZ chicks (Table 10), were calculated for each chick and averaged over all the chicks for each institution. This did not account for all of the time recorded for DZ chicks, as behaviors that were recorded in the EthoTrak study but not in the SNZP chick data were not included. However, the included behaviors added up to 98.2% of the DZ chicks' time. Kruskal-Wallis tests were used to compare each of the behaviors between the two locations.

Data Set

Five chicks (all males) from two sires were raised by one dam (studbook (SB) #131) at DZ during the EthoTrak study (Table 11). One of these chicks died at 16 days; the rest survived at least through the end of their first year. Two of these chicks were from the same clutch. Only the four chicks that survived to eight weeks were included in the analysis.

Seventeen chicks (6 males, 11 females) were hand-raised by the keepers at the SNZP between 2008 and 2015 (Table 11). These chicks were from two pairs: 15 from SB #143/ SB #389 and two from SB #680/ SB #681. Between one and four chicks were raised each year, with an average of 2.4 chicks/year. The majority were raised with at least one sibling.

Table 11: Chicks in Behavior Comparison.

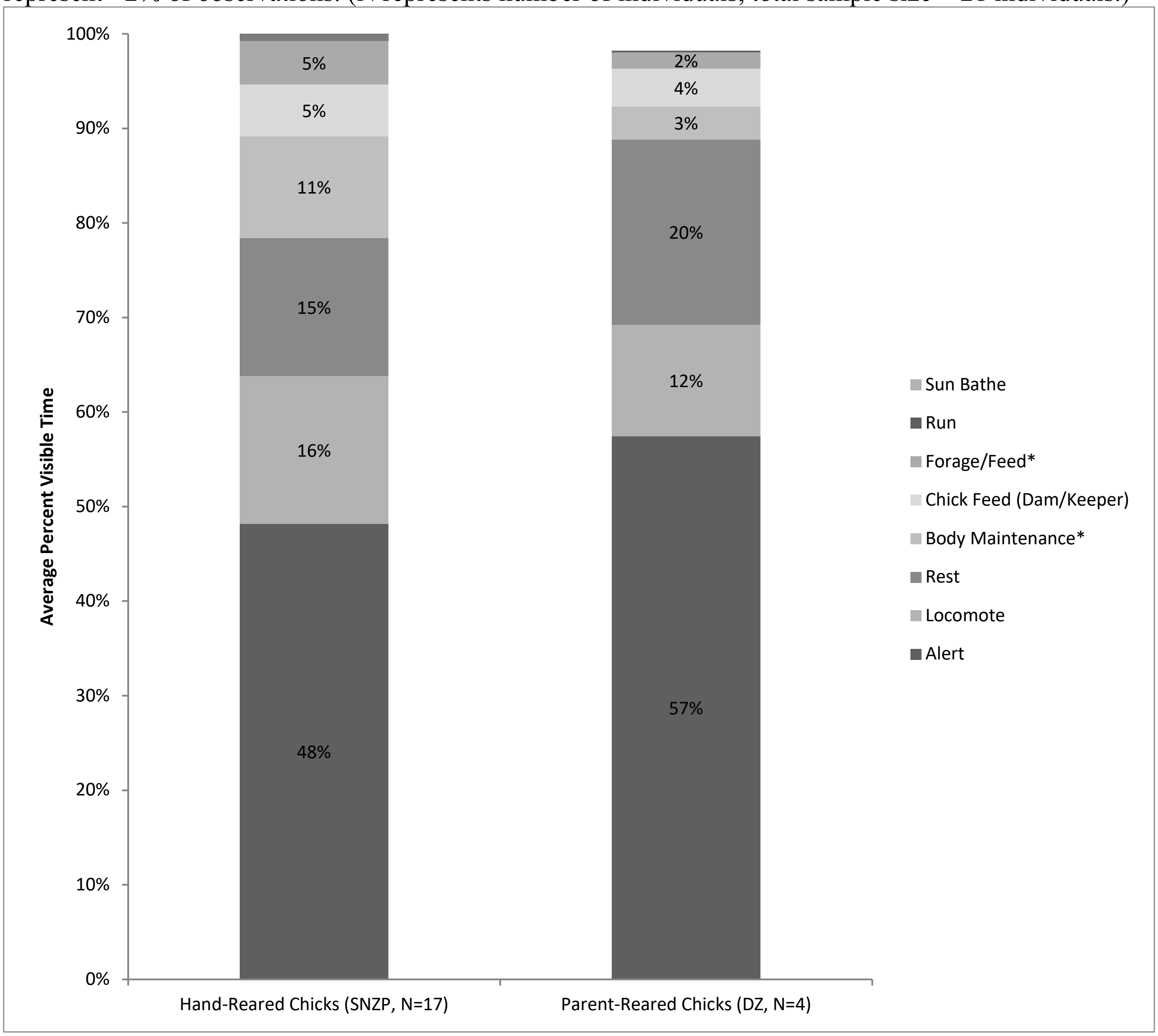
Institution/ Rearing	Studbook #	Sex	Hatch Date	Death Date	Sire Stdbk #	Dam (Stdbk #)
DZ/Parent	652	M	6/11/2007	5/1/2012	370	131
	673*	M	5/4/2008	5/20/2008	370	131
	679	M	7/5/2008		370	131
	680	M	7/5/2008		370	131
	689	M	6/28/2009	4/9/2010	152	131
SNZP/Hand	676	M	6/28/2008		143	389
	677	F	6/29/2008		143	389
	681	F	6/17/2008		143	389
	682	M	6/17/2008	1/16/2012	143	389
	686	F	6/22/2009	9/28/2009	143	389
	687	M	6/23/2009		143	389
	704	M	6/5/2010	5/11/2011	143	389
	705	F	6/6/2010	6/27/2014	143	389
	706	F	6/21/2010		143	389
	707	F	6/22/2010	10/6/2010	143	389
	735	M	6/3/2011		143	389
	737	M	6/15/2011		143	389
	739	F	6/9/2012		143	389
	740	F	6/10/2012	5/17/2013	143	389
	743	F	6/5/2013		143	389
	763	F	6/8/2015		680	681
	764	F	6/24/2015		680	681

*This individual was not included in the analysis, as he did not survive to be 8 weeks old.

Results

Overall, HR and PR chicks spent similar amounts of time on most behaviors (Figure 8). HR chicks spent significantly more time on body maintenance (H_1=7.2, P=0.01) and foraging/feeding (H_1=6.5, P=0.01). Note that foraging/feeding includes looking for food but does not include being fed by the dam or keepers. Both sets of chicks spent approximately the same amount of time being fed by the dam or the keepers.

Figure 8: Activity Budget of Hand and Parent-Reared Chicks
The difference between behaviors marked with a * was significant ($P<0.05$) by Kruskal-Wallis test. See text for explanation of the differences in "Alert" and "Rest", which were not significant. Unlabeled boxes represent <2% of observations. (N represents number of individuals, total sample size = 21 individuals.)



PR chicks spent more time alert and resting but neither difference was significant. The larger amount of time the PR chicks spent on each of these behaviors was primarily driven by one individual (see Appendix A.6). For alert, that individual was SB #689, who was alert 77% of the time. Without SB #689, the PR chicks' average time alert was 51% (compared to 45% for HR). For rest, that individual was SB

#673, who rested 45% of the time. Without SB #673, the PR chicks' average time resting was 11% (compared to 14% for HR).

4.4 Adult Behavior

Methods

The adults in the EthoTrak study (see Section 2) were classified as a) hand-reared, b) parent-reared, or c) wild-caught. Adult behavior was investigated by rearing method, separately by sex and by season. Statistical analysis was done in R v3.2.3 in the same way as the Activity Budget analysis (see section 2.1). Mixed effect models were used to examine the effects of season, sex, and rearing on each behavior. Year, Institution, and Individual Identity were again included as random effects. As above, we report t-statistics because the estimated regression coefficients calculated by the mixed effects models followed a Student-t distribution. As before, averages for figures were determined by first calculating an institutional average across all individuals at that institution. The figures were then produced by averaging over all institutions in each condition and calculating the standard error across institutions.

Data Set

Of 32 adult birds (14 males, 18 females) used in the analysis, 13 were hand-reared (HR), 5 were parent-reared (PR), and 14 were wild-caught (WC). The average number of weekly observations per individual was 126 (max=303, min=6). The total dataset included 4,041 weekly averages.

Results

Overall, the behavior of birds was very similar across rearing types (Figure 9). HR birds rested alert slightly more often than other birds (vs. WC: $t=-2.2$, $p=0.03$; vs. PR: $t=-1.9$, $p=0.06$). To investigate whether an influence of sex or season was concealing differences between types of rearing, we added those variables to the analyses. Male WC birds rested alert more than other males ($t=2.65$, $P=0.009$).

There were no differences in sexual or maternal behavior by rearing (Figure 10). Although Figure 10 shows an apparent difference in maternal behavior between HR, PR, and WC females, this difference is not significant. This is because there was a great deal of variation in how much time each individual spent on maternal behavior: individual identity (ID) accounted for 95% of the variation. Six of the nine WC females in the sample spent less than 5% of their time on maternal behavior during the breeding season. The amount of time the final three spent varied widely as well: 17%, 30%, and 48%.

Figure 9: Activity Budget of Hand-Reared, Parent-Reared, and Wild-Caught Adults
The difference between rearing categories for behaviors marked with a * was significant (P<0.05) by 3-way mixed-model analysis. Unlabeled boxes represent ≤2% of observations. (N represents number of individuals, total sample size = 40 individuals.)

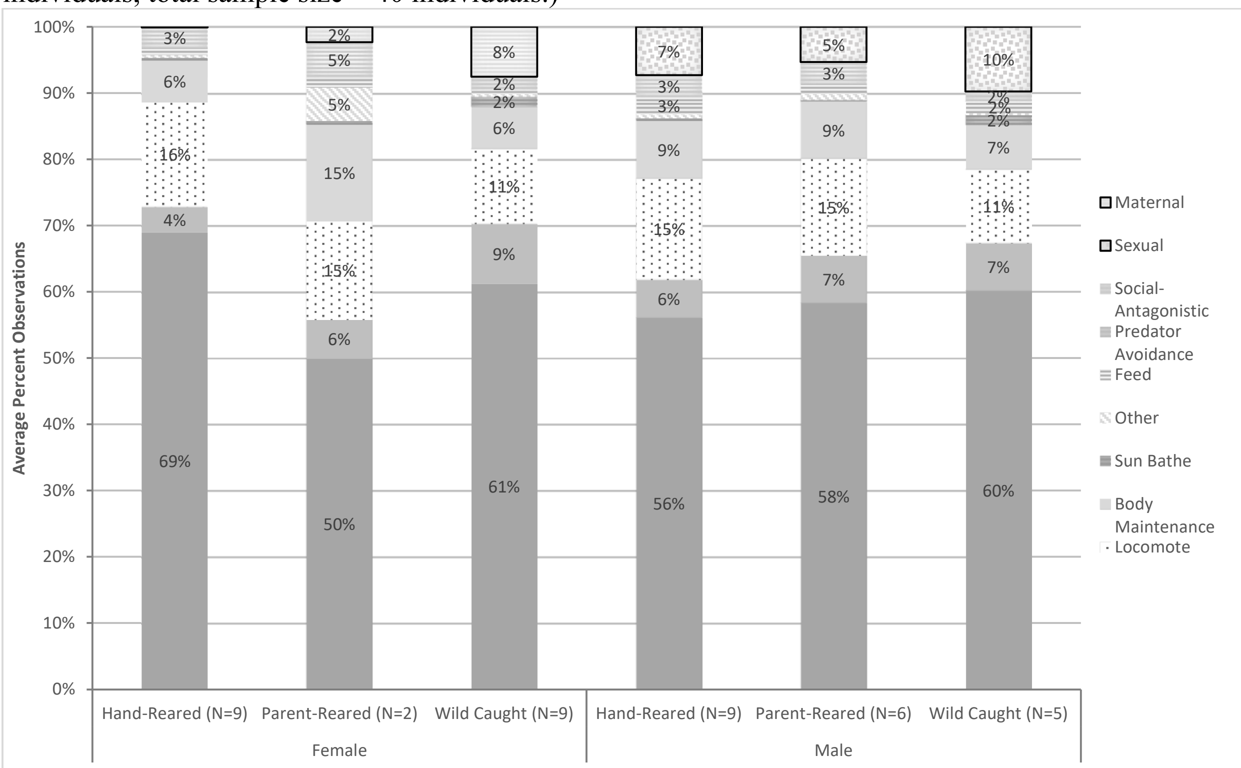
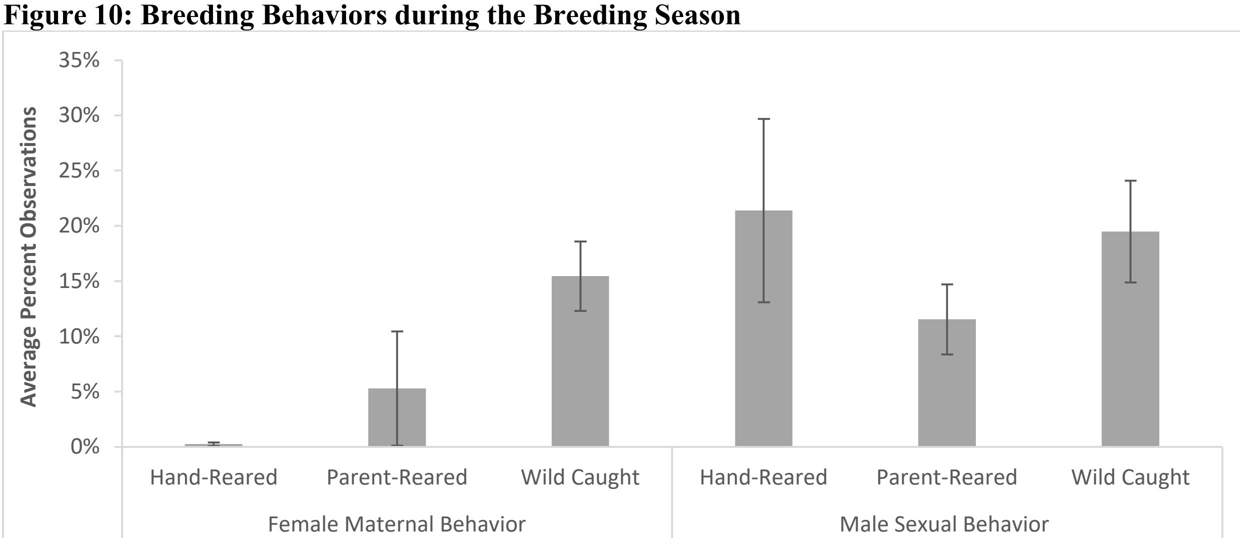


Figure 10: Breeding Behaviors during the Breeding Season



4.5 Fecundity

Methods

The breeding success of birds that were a) hand-raised, b) parent-raised, or c) wild-caught was compared using the same 21 May 2016 search of the 2016 studbook as the chick survival analysis. Breeding success was defined as the proportion of chicks surviving to three years of age. Chicks younger than three years at the time of the search were again excluded from the dataset, which therefore included only chicks hatched through 2012. Differences by rearing of the dam and sire were tested separately using non-parametric Kruskal-Wallis tests.

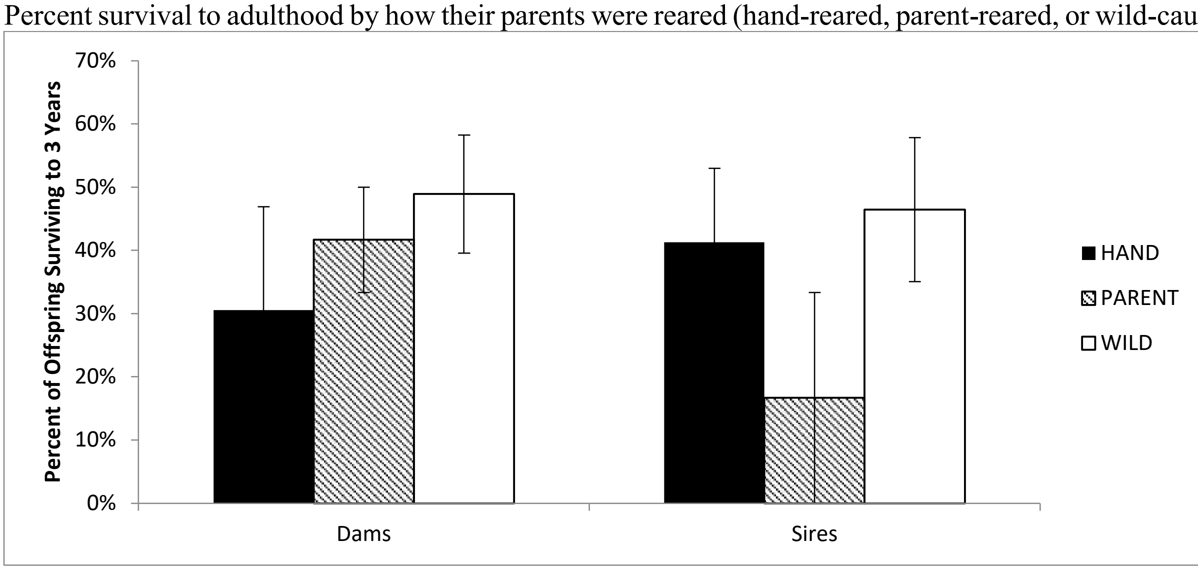
Data Set

The breeding success of 17 dams and 18 sires was evaluated based on how they had been raised. The dams included 9 WC birds, 6 HR birds, and 2 PR birds. The sires included 9 WC birds, 7 HR birds, and 2 PR birds.

Results

There were no significant differences in breeding success by the rearing of either dams or sires (Dams: KW_2=1.6, P=0.45; Sires: KW_2=1.8, P=0.41; Figure 12). Breeding of HR, PR, and WC birds were all equally successful in producing chicks that survived to be adults.

Figure 12: The Impact of the Parents' Rearing on Chick Survival
Percent survival to adulthood by how their parents were reared (hand-reared, parent-reared, or wild-caught).



4.6 Discussion

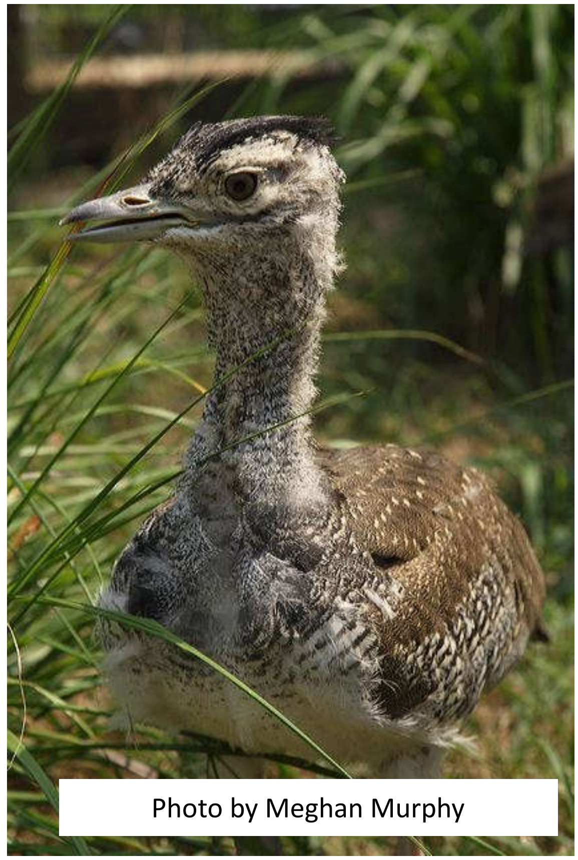


Photo by Meghan Murphy

Both hand-rearing and parent-rearing of kori bustards within AZA accredited facilities are equally successful methods of producing chicks that survive to be successfully breeding adults. Hand- and parent-reared chicks behave equivalently as both chicks and adults. Chicks of both sexes born to hand-reared and parent-reared chicks survive to adulthood at equivalent rates to each other and to the chicks born to wild-caught birds.

Chick Survival

Overall, 50% (75/151) of kori bustard chicks reared in the United States survived to be adults, compared to wild populations where first year survival is 20% (Osborne and Osborne 2004). When compared to a related taxa, ten managed crane populations (n=914 individuals) within the United States survivability to adulthood was similar (K. Melton, personal communication 2017). In the buff-crested bustard (*Lophotis gindiana*) population in the US, 54% of males survive to adulthood whereas 61% of females survive (Hallager and Ballou, 2015b). There were no significant differences in survival of kori bustard chicks by rearing or sex (see Table 8).

Previous studies have shown a similar lack of impact of rearing methods on survival in other bird species. For example, Kreger *et al*. (2006) demonstrated that rearing methods did not affect survival in hand-reared vs. parent-reared whooping cranes (*Grus americana*). Similarly, studies have also shown no difference in survival between parent-reared and hand-reared houbara bustard *Chlamydotis undulata* (Van Heezik and Seedon, 1998), killdeer *Charadrius vociferous* (Powell and Cuthbert, 1993), common raven *Corvus corax* (Valutis and Marzluff, 1999) and tawny owl *Stix aluco* (Bennett and Routh, 2000). Likewise, Hill and Robertson (1988) found no differences between wild and hand-reared female ring-necked pheasant

(*Phasianus colchicus*) in the number of nesting attempts or proportion of successful nests, although wild females were four times more productive than hand-reared females. Kreger (2005) cited several studies that dispute the presumed advantage of parent-reared animals demonstrating that hand-reared and parent-reared birds have equal likelihoods of survival in the wild (Powell and Cuthbert, 1993; Valutis and Marzluff ,1999; Van Heezik *et al*., 1999; Bennett and Routh, 2000).

Chick Behavior

Overall, hand-reared (HR) and parent-reared (PR) kori bustard chicks spent similar amounts of time on most behaviors. Van Heezik and Seddon (1998) observed hen-reared (PR) houbara bustard chicks spent more time walking than hand-reared chicks. They suggested that the lack of a hen gave hand-reared chicks less motivation to move (Van Heezik and Seddon, 1998). We did not see a difference in locomotion in the current results, however.

HR kori bustard chicks in the current study, on the other hand, spent significantly more time on body maintenance, perhaps because they did not have the interaction with the hen that PR chicks did. White (2012) noted that preening was first observed in mother-reared (PR) Australian bustard chicks at 8 days, coinciding with the growth of pin feathers. When the mother preened, the chick preened as well, possibly stimulated by watching the mother. Hand-reared Australian bustard chicks were not seen preening until reaching a much more advanced stage of development. In the current study, HR kori bustard chicks were first observed preening in days 7 to 10. Unlike the Australian bustards, these birds did not appear to need the stimulation of the mother, or the growth of their pin feathers, to begin preening. Van Heezik and Seddon (1998) also observed hand-reared houbara chicks preening at 4 days compared to 8 days in parent-reared chicks. The lack of preening in PR kori bustard chicks, who were first observed doing body maintenance in week three, may also be methodological. Rare behaviors like preening are sometimes missed by the sampling methods used in the EthoTrak study.

HR chicks also spent significantly more time foraging/feeding than PR chicks. White (2012) observed that PR Australian bustard chicks spent on average 10% of their time on feeding between the ages of 9-30 days. Compared with exercise and resting, feeding occupied a small proportion of the overall time budget in the current study (5% for HR, 2% for PR). Bai-Lian *et al*. (2007) observed hand-reared great bustard chicks (*Otis tarda dybowskii*) spent about 2% of their time foraging from hatching to 8 weeks, similar to the PR chicks in the current study.

Adult Behavior and Breeding Success

Overall, HR, PR, and wild-caught (WC) adults spent similar amounts of time on most behaviors. A few differences were noted, however. HR birds rested alert, perhaps because of their comfort with humans, such as the person collecting the data. PR and WC birds, while still familiar with the data collector, may be less comfortable with humans in general.

In a similar finding, White (2012) noted that hand-reared Australian bustards (*Ardeotis australis*) appeared to lose their domestication quickly once released into natural enclosures. He further noted that hand-reared Australian bustards did not exhibit the same tendency to imprint on humans as do cranes or geese under similar conditions. He also found that hand-reared birds became more independent with age and assumed similar behavior to wild caught birds in human care, as was seen with the kori bustards in the current study.

Although no HR females and only one PR female bred during the EthoTrak study, the studbook analysis clearly shows that HR and PR females successfully bred at other times.

Conclusions

The kori bustard SSP seeks to establish a genetically viable and self-sustaining *ex situ* population, which will require breeding of additional founder and under-represented birds (Hallager and Ballou, 2015a). We found no difference in breeding success between kori bustards imported from the wild and those born in US zoos. We similarly found no differences in breeding success or behavior between hand-reared and parent-reared kori bustards. This suggests that if a genetically viable population can be established, the future existence of kori bustards in US zoos need not rely on imports from wild populations. This also indicates that both hand-rearing and parent-rearing of kori bustards are successful strategies to increasing the *ex-situ* population.

5. Management Recommendations

Even though we had a relatively large sample size of 50 birds at nine institutions, a relatively small subset were breeding individuals. This study had tremendous variation between institutions which made finding significant results difficult for many of the questions. Thus, further study of environmental or management factors may shed some light on this disparity.

5.1 Social housing

- Even though a single pair of kori bustards can breed, for institutions holding a pair that are not breeding, housing a second male in acoustic contact may stimulate more display behavior and lead to higher breeding success. Focused studies on before-after the addition of a second male would be beneficial in further elucidating this effect. It would be worth investigating whether playing the sounds of displaying males in the vicinity of females is sufficient to stimulate egg laying in kori bustards under human care.
- Females in visual contact may have higher breeding success than those housed without other females or housed in physical contact. This also needs further study because the effect was driven by the Dallas Zoo. Again before-after studies could be beneficial.
- A long-standing recommendation by the kori bustard SSP has been that kori bustards should not be housed with hoofstock. As documented in our study, managers should exercise caution when housing kori bustards with other bird species. Future studies in this area of research that could tease apart the influence of heterospecifics, exhibit size, and management techniques would be very beneficial.
- This study could not determine the true effect of crowd levels on breeding kori bustards. Future research is needed.

5.2 Rearing-method

- We found that hand-rearing and parent-rearing produced similar results. Hand rearing may be necessary for increasing productivity of genetically valuable individuals. However, parent-rearing is acceptable, especially when staffing and resources are limited and predation is not an issue.

6. References

AZA Gruiformes TAG. 2020. Bustard (Otididae) Care Manual (2nd ed.). *AZA*, Silver Spring, MD.

Bai-Lian, Z., Xiu-Hua, T., Qun-Xiu, L., Xiang-Bao, H. and Xue-Feng, M. 2007. Research on Behavior Development and Daily Rhythm of Captive Great Bustard Nestlings. *Chin J of Zoology* 42(6): 57-63.

Bennett, J.A. and Routh, A.D. 2000. Post-release survival of hand-reared tawny owls (*Strix aluco*). *Animal Welfare* 9: 317-321.

BirdLife International. 2016. *Ardeotis kori*. *The IUCN Red List of Threatened Species 2016*.

Bird, T and Johnson, G. 2001. Teaching birds to sing. Proceedings 5th International conference on Environmental Enrichment, Sydney, Australia, 4 – 9th November, Taronga Zoo.

Bradbury, J. 1981. The evolution of leks. In, R.D. Alexander & D.W. Tinkle (Eds.): *Natural selection and social behaviour*, pp. 138-169. Chiron Press. New York and Concord.

Deviche P. 2014. Reproductive Behavior. In *Sturkie's Avian Physiology, 6th Edition* (Ed. C. Scanes), Elsevier, pp. 695-715.

Great Bustard Group Members Update June 2020. Newsletter of the Great Bustard Group http://greatbustard.org/

Gregson, J. 1986. Breeding the Little Black Bustard *Eupodotis afra* at the Paignton Zoological & Botanical Gardens. *Avicultural Magazine* 92:61–63

Hallager, S. and Boylan, J. (eds). 2004. *Kori Bustard AZA Husbandry Manual.*

Hallager, S. and Ballou, J. 2015. *Buff-crested Bustard SSP Breeding and Transfer Plan*.

Hallager, S. 2017. International Studbook for the kori bustard *Ardeotis kori.* Smithsonian National Zoological Park.

Hallager, S. 2018. Population Analysis & Breeding and Transfer Plan for the Kori Bustard *Ardeotis kori*. Smithsonian National Zoological Park.

Hanselmann, R., Hallager, S., Murray, S., and Mazet, J. 2013. Causes of Morbidity and Mortality in Captive Kori Bustards (*Ardeotis kori*) in the United States. J of Zoo and Wildlife Medicine 44: 348–363.

Hill, D. and Robertson, P. 1988. Breeding Success of Wild and Hand-Reared Ring-Necked Pheasants. *J Wildlife Management* 52(3): 446-450.

Hurd C. R. 1996. Interspecific attraction to the mobbing calls of black-capped chickadees (*Parus atricapillus*). *Behav Ecol Sociobiol* 38:287–292

Hutchins, M., Sheppard, C., Lyles, A. and Casedi, G. 1995. Behavioral Considerations in the Captive management, propagation and reintroduction of endangered birds. In: Gibbons, E.F., Durreant, B.S., Demarest, J. (Eds). *Conservation of Endangered Species in Captivity: An Interdisciplinary Approach*. State University of New York Press, Albany, NY., p 263-289.

Jhala, Y. V., Dutta, S., Karkarya, T., Awasthi, A. Bipin, C.M. *et al*. 2020. *Habitat improvement and conservation breeding of the Great Indian bustard: and integrated approach. Progress Report* April 2018-March 2020. Wildlife Institute of India, Dehradun 248001, India. | TR/2020/03

Johnsgard, Paul A. 1991. *Bustards, Hemipodes, and Sandgrouse, Birds of Dry Places*. Oxford University Press

King C.E. 1993. Environmental enrichment: is it for the birds? *Zoo Biol* 12:509–512.

Kleiman, D.G. 1996. Reintroduction programs. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.). *Wild Mammals in Captivity: Principles and Techniques*. University of Chicago Press, Chicago, p297-305.

Kreger, M., Hatfield, J., Estevez, I., Gee, G. and Clugston. D. 2005. The effects of captive rearing on the behavior of newly-released whooping cranes (*Grus americana*). *Appl Anim Behav Sci* 93(1): 165-178.

Kreger, M., Hatfield, J., Estevez, I., Gee, G. and Clugston, D. 2006. Behavioral Profiles of the Captive Juvenile Whooping Crane as an Indicator of Post-Release Survival. *Zoo Biol* 25: 11-24.

Lictenberg, E.M. and Hallager, S. 2007. A description of commonly observed behaviors for the kori bustard (*Ardeotis kori*). *Journal of Ethology* 26 (10): 17-34.

Mmassy, E. C., Fyumagwa, R. D., Jackson, C. R., Bevanger, K. and Røskaft, E. 2017. Kori bustard (*Ardeotis kori struthiunculus)* occurrence in the Serengeti grass plains, northern Tanzania. *Afr. J. Ecol.*, 55: 298-304.

Morales, M.B., Juguet, F., and Arroyo, B. 2001. Exploded leks: What bustards can teach us. *Ardeola* 48: 85-98.

Osborne, T. and Osborne, L. 1998 Ecology of the Kori bustard in Namibia. *Annual Report of the Ministry of Environment and Tourism Permit Office*, Namibia.

Osborne, T. and Osborne, L. 2004 Ecology of the Kori bustard in Namibia. *Annual Report of the Ministry of Environment and Tourism Permit Office*, Namibia.

Penfold, L., Hallager, S., Boylan, J., de Wit, M., Metrione, L. and Oliva, M. 2013. Differences in Fecal Androgen Patterns of Breeding and Nonbreeding Kori Bustards (*Ardeotis kori*). *Zoo Biology* 32: 54-62

Pepperberg I.M. 1981. Functional vocalizations by an African Grey parrot (*Psittacus erithacus*). *Z Tierpsychol* 55:139–160.

Perkins, D.R. IV. 2012. *Forecasting Tourist Decisions Regarding Zoo Attendance Using Weather and Climate References*. (Master's thesis) University of North Carolina at Chapel Hill.

Petrie, M. and Williams, A. 1993. Peahens lay more eggs for peacocks with larger trains. *Proc. R. Soc. Lond. B.* 251:127–131.

Powell, A. and Cuthbert, F. 1993. Augmenting small populations of plovers: an assessment of cross-fostering and captive rearing. *Conservation Biology* 7: 160-168

Rosenberger J, Kowalczyk A, Łukaszewicz E, and Strzała T. 2020. Female-Male and Female-Female Social Interactions of Captive Kept Capercaillie (*Tetrao Urogallus*) and Its Consequences in Planning Breeding Programs. *Animals* 10(4):583.

Senyatso, K., Collar, N.J., and Dolman, P. 2012. Assessing range-wide conservation status change in an unmonitored widespread African bird species. *Diversity and Distribution* 1-14.

Snyder, N., Derrickson, S., Bessinger, S., Wiley, J., Smith, T., Toone, W., and Miller, B. 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology* 10: 338-248.

Stevens, E. F. 1991 Flamingo breeding: the role of group displays. *Zoo Biology* 10 (1): 53-63.

Valutis, L. and Marzluff, J. 1999. The appropriateness of puppet-rearing birds for reintroduction. *Conservation Biology* 13: 584-591.

van Heezik, Y. and Seddon, P. 1998. Ontogeny of behavior of hand-reared and hen-reared captive houbara bustards. *Zoo Biology* 17: 245-255.

van Heezik, Y., Seddon, P. and Maloney, R. 1999. Helping reintroduced houbara bustards avoid predation: effective anti-predator training and the predictive value of pre-release behavior. *Anim Cons* 2: 155-163

Watters, J.V., Margulis, S.W., Atsalis, S., 2009. Behavioral monitoring in zoos and aquariums: A tool for guiding husbandry and directing research. *Zoo Biology*, 28, 35-48.

White, D. 2012. *The Australian Bustard Breeding and Management in Captivity*.

7. Acknowledgements

We thank the animal management staff and volunteers at all the zoos (Birmingham Zoo, Cheyenne Mountain Zoo, Dallas Zoo, Living Desert Zoo, Phoenix Zoo, Smithsonian National Zoological Park, White Oak Conservation Center, Zoo Atlanta, and Zoo Miami) that took data for and assisted with this project. We would also like to thank the Kori SSP for funding this project. Thank you to Kayla Melton, Population Management Center & Alexander Center for Applied Population Biology, Lincoln Park Zoo for analyzing crane program data. Thank you to Cynthia Bennett, Marcie Herry, Jenny Tibbott, and Katie Vyas for insightful reviews that improved the manuscript.

A. Appendices

A.1 Percent of Females Laying

Zoo	Year	# Females	Percent of Females Laying
BZ	2008	1	0%
	2009	1	0%
	2010	1	100%
	2011	1	100%
	2012	1	100%
CMZ	2008	2	0%
	2009	2	0%
DZ	2007	3	100%
	2008	3	100%
	2009	3	100%
	2010	3	67%
	2011	3	100%
	2012	3	67%
LDZ	2007	1	0%
	2008	1	0%
	2009	1	0%
	2010	1	0%
	2011	1	0%
	2012	1	0%
SNZP	2007	4	50%
	2008	3	67%
	2009	3	33%
	2010	3	33%
	2011	5	20%
	2012	3	33%
WOCC	2008	1	0%
	2009	1	0%
	2010	1	0%
ZA	2010	1	0%
ZM	2008	3	67%
	2009	3	0%
	2010	3	0%

A.2 Female-Female Contact

F-F Access	Zoo	Year	# Females	Percent of Females Laying	Average Clutches/Female
Alone	**BZ**	2008	1	0%	0.0
		2009	1	0%	0.0
		2010	1	100%	1.0
		2011	1	100%	2.0
		2012	1	100%	2.0
	CMZ	2008	2	0%	0.0
		2009	2	0%	0.0
	LDZ	2007	1	0%	0.0
		2008	1	0%	0.0
		2009	1	0%	0.0
		2010	1	0%	0.0
		2011	1	0%	0.0
		2012	1	0%	0.0
	WOCC	2008	1	0%	0.0
		2009	1	0%	0.0
		2010	1	0%	0.0
	ZA	2010	1	0%	0.0
Visual	**DZ**	2007	3	100%	3.5
		2009	3	100%	4.5
		2010	3	67%	3.3
		2011	3	100%	3.3
		2012	3	67%	3.7
	ZM	2008	3	67%	1.3
		2009	3	0%	0.0
		2010	3	0%	0.0
Physical	**SNZP**	2007	4	50%	0.8
		2008	3	67%	1.3
		2009	3	33%	0.7
		2010	3	33%	1.0
		2011	5	20%	0.2
		2012	3	33%	0.3

A.3 On vs Off Exhibit

On/Off	Zoo	Year	Average Clutches/Female
OFF	**BZ**	2008	0.0
		2009	0.0
		2010	1.0
		2011	2.0
		2012	2.0
	DZ	2007	3.5
		2009	4.5
		2010	3.3
		2011	3.3
		2012	3.7
	LDZ	2007	0.0
		2008	0.0
	WOCC	2008	0.0
		2009	0.0
		2010	0.0
	ZM	2008	1.3
		2009	0.0
		2010	0.0
ON	**LDZ**	2009	0.0
		2010	0.0
		2011	0.0
		2012	0.0
	SNZP	2007	0.8
		2008	1.3
		2009	0.7
		2010	1.0
		2011	0.2
		2012	0.3
	ZA	2010	0.0

A.4 Crowd Size vs Female Laying (SNZP only)

A.4.1 Percent of Females Laying

Year	Average Crowd	# Females	Percent of Females Laying
2007	5.4	4	50%
2008	9.5	3	67%
2009	10.3	3	33%
2010	10.3	3	33%
2011	12.9	5	20%
2012	14.9	3	33%

A.4.2 Clutches per Female

Studbook #	Year	Average Crowd	Clutches Laid
87	**2007**	5	0
	2008	10	1
	2009	10	0
	2010	10	0
95	**2007**	4	0
115	**2007**	5	1
	2008	9	0
	2009	10	0
	2010	10	0
389	**2007**	5	2
	2008	10	3
	2009	10	2
	2010	10	3
	2011	13	1
	2012	15	1
677	**2012**	15	0
681	**2012**	15	0

A.5 Time Spent on Maternal Behavior (females that laid only)

Zoo	On/Off Exhibit	Studbook #	Year	Percent Time Spent on Maternal Behavior
BZ	**OFF**	546	2010	0%
			2011	0%
			2012	21%
DZ	**OFF**	57	2007	72%
			2008	38%
			2009	38%
			2010	35%
			2011	2%
			2012	27%
		131	2007	87%
			2008	57%
			2009	85%
			2010	65%
			2011	82%
		136	2007	8%
			2008	5%
			2009	21%
		623	2011	5%
			2012	49%
SNZP	**ON**	87	2008	20%
		115	2007	0%
		389	2007	46%
			2008	79%
			2009	77%
			2010	39%
			2011	0%
			2012	100%

A.6 Activity Budgets for PR & HR Chicks

Zoo	Chick	Alert	Locomote	Rest	Body Maintenance	Chick Feed	Forage/ Feed	Run	Sun Bathe
SNZP (HR)	**C2008-1**	45%	16%	9%	17%	8%	4%	1%	0%
	C2008-2	48%	14%	11%	16%	9%	2%	0%	0%
	C2008-3	52%	18%	8%	7%	7%	6%	1%	1%
	C2008-4	50%	17%	10%	10%	7%	6%	1%	0%
	C2009-1	43%	14%	12%	19%	4%	7%	1%	0%
	C2009-2	40%	21%	10%	17%	3%	8%	1%	0%
	C2010-1	39%	24%	20%	10%	3%	4%	0%	0%
	C2010-2	39%	28%	16%	11%	3%	2%	0%	0%
	C2010-3	38%	21%	27%	6%	4%	3%	0%	0%
	C2010-4	41%	17%	24%	8%	4%	6%	0%	0%
	C2011-1	51%	9%	19%	10%	4%	3%	0%	2%
	C2011-2	43%	11%	21%	10%	5%	7%	2%	1%
	C2012-1	51%	13%	12%	10%	8%	6%	0%	0%
	C2012-2	59%	10%	10%	9%	8%	5%	0%	0%
	C2013-1	67%	6%	12%	7%	3%	4%	0%	0%
	C2015-1	57%	10%	15%	9%	7%	3%	0%	0%
	C2015-2	55%	16%	13%	7%	6%	3%	0%	0%
DZ (PR)	**673**	42%	5%	45%	0%	6%	1%	0%	0%
	679	52%	21%	11%	8%	6%	1%	0%	0%
	680	58%	17%	13%	2%	4%	1%	1%	0%
	689	77%	3%	9%	4%	0%	4%	0%	0%