# Seasonal fluctuations in population size and habitat segregation of Kittlitz's Plover *Charadrius pecuarius* at Barberspan Bird Sanctuary, North West province, South Africa

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Seasonal fluctuations in population size reflect breeding patterns and movements of birds, but distinguishing residents from itinerant birds is difficult with partially migratory species such as Kittlitz's Plover. We determined changes in the size of Kittlitz's Plover populations in two microhabitats (Goose Point and Sandy Beach) at Barberspan Bird Sanctuary, North West province, South Africa, where we ringed waders between February 2008 and May 2010. Using a Bayesian model, we estimated the population of this species at these two sites from capture–recapture data gathered in eight 3- to 12-day collection periods. The estimated adult population at Goose Point peaked at 161 in October 2009, but decreased to about 40 in March 2009 and March 2010. The immature population peaked at 119 in January–February 2010. This, along with observations of nests and chicks, suggests that residents bred at Goose Point from September to March. The estimated number of adults at Sandy Beach increased from 48 in March 2010 to 380 in April 2010. Adults captured there in April 2010 formed feeding flocks and were heavier than the resident birds at Goose Point. These results suggest that Barberspan Bird Sanctuary supports resident and itinerant populations that are partially segregated in different microhabitats.

# Introduction

Many species of waders in Africa are sedentary in part of their range, but also have populations that undertake intra-African movements (Delaney et al. 2009). Depending on environmental conditions, such as local rainfall or temperature, a species might comprise sedentary, nomadic and migratory populations (Lundberg 1988, Pulido 2007). Varying geographic conditions, the erratic timing of rainfall and other environmental factors that trigger population movements limit our understanding of the movement patterns even of common waders (Underhill et al. 1999, Tree 2001, Roshier et al. 2002, Kraaijeveld 2008). Kittlitz's Plover Charadrius pecuarius is a model example of this problem. It is a common breeding bird in sub-Saharan Africa and in the Nile Valley, but its movement patterns are poorly understood (Urban 1986, Turpie and Tree 2005). Populations from the coastal and eastern regions of South Africa, Swaziland and southern Mozambigue are thought to be sedentary, but populations in the interior of southern Africa are considered migratory or nomadic, and their movements are irregular and depend on seasonal rainfall (Tree 1997, Underhill et al. 1999, Tree 2001, Turpie and Tree 2005, Dodman and Parker 2009). Furthermore, after long-distance flights, migratory populations might become locally nomadic within the staging area (Turpie and Tree 2005).

Ringing recoveries of Kittlitz's Plover do not reflect the extent of this species' movements. The longest movement recorded of a ringed bird is 332 km within Zimbabwe, but this species is expected to move several thousands of kilometres (Tree 1997, Underhill et al. 1999). The Kittlitz's Plover's breeding season varies geographically and can last up to 10 months, depending on rainfall and the related availability of food and habitat (Tree 1997, Turpie and Tree 2005). The migrants supplement resident populations, so influxes of non-residents into a location are not easily detected (Tree 2001). Barberspan Bird Sanctuary in North West province, South Africa, supports a regular breeding population of Kittlitz's Plovers and also hosts irregular influxes of nomads or migrants in some years (Farkas 1962, Milstein 1975).

In this paper we estimate seasonal fluctuations in the size of Kittlitz's Plover populations at Barberspan Bird Sanctuary using a capture-recapture analysis, supported by analyses of these birds' measurements. We intend this to be a case study testing the utility of this method to distinguish local and itinerant populations of waders at a site. We also discuss the spatial and behavioural segregation of resident and itinerant Kittlitz's Plovers at different microhabitats in Barberspan Bird Sanctuary.

# Materials and methods

## Study site and methods of data collection

We captured Kittlitz's Plovers at Barberspan Bird Sanctuary (26°33' S, 25°36' E; Figure 1), one of South Africa's original Wetlands of International Importance in terms of the Ramsar Convention, and recognised as an Important Bird Area by BirdLife International (Cowan 1995, Barnes 1998). The waterbody at Barberspan varies in area from 257 ha to 2 000 ha depending on rainfall (Milstein 1975, Barnes 1998, North West Parks and Tourism Board 2010). The lake is fed by the Harts River and is the main permanent waterbody in a vast area when the hundreds of local pans dry up in winter and during periods of drought (Milstein 1975, Allan et al. 1995). The Barberspan waterbody is shallow and alkaline (pH range 8.2-9.4: Farkas 1962, Milstein 1975). It features open mudflats, short grasslands, patches of tall reedbeds in summer, and acacia thickets around its banks. Peninsulas and bays around the lake provide different microhabitats for Kittlitz's Plovers. Goose Point (Figure 1) is a secluded peninsula with patches of short grass strewn with large pebbles and a muddy shoreline. Sandy Beach, a section of the sanctuary where fishing is allowed, features a flat sandy beach with medium-length grass and a muddy shoreline. The muddy banks of Botany Bay and Godwit Bay are bordered by short grass interspersed with pebbles and by patches of reeds. The habitat near the Bird Hide is mainly determined by water level but usually consists of extensive mudflats surrounded by patches of tall reeds.

We captured and ringed Kittlitz's Plovers in a series of expeditions between 26 February 2008 and 1 May 2010 (Table 1). We chose two main ringing sites, Goose Point and Sandy Beach (Figure 1), for the capture-recapture sessions, which provided data for estimating the population sizes at these locations. We also occasionally ringed waders at Botany Bay, Godwit Bay and near the Bird Hide (Figure 1). We used data from ringing sessions at these five locations to trace movements of Kittlitz's Plovers within the reserve (Figure 1). We caught waders in 2-10 mist nets positioned perpendicular to the shoreline and opened the nets from sunset to about 2 h after sunrise, on some nights with a break between 00:00 and 04:00. We supplemented mistnetting with 30-32 wader traps of a Polish design (Meissner 1998), set up on the shore and open continuously. The mistnets were checked every hour and the traps every 2 h. Goose Point peninsula (Figure 1), where we trapped waders most often but which was under the highest predation pressure from black-backed jackals Canis mesomelas, was closed off with an ineffective wire fence supplemented in 2010 by an electric jackalproof fence.

At first capture each bird was ringed, aged and several measurements were taken: total head length, bill length, tarsus length, all measured with callipers to 0.1 mm accuracy, and tarsus-and-toe length and wing length measured with a stopped ruler to 1 mm accuracy (Meissner 2008). At each capture birds were weighed on a digital scale accurate to 1 g, the fat score was assessed according to the scale proposed for waders by Meissner (2009), and the moult of primaries was described by the standard 0–5 scale (Ashmole 1962, de Beer et al. 2001). After ringing



Figure 1: Location of ringing sites at Barberspan Bird Sanctuary. Symbols show the location of mist nets (triangles) and wader traps (circles); arrows show the directions of movements of birds from one site to another and values near each arrow indicate the number of times this was observed.

and measuring, the birds were released close to the site at which they had been trapped. Measurements were taken by MR. Kittlitz's Plovers were aged by plumage as described by Tree (1973). Immature birds were distinguished from adults in non-breeding plumage by pale edges to the upperwing coverts and often to the back feathers, and by a less contrasting facial pattern than that of adults (Tree 1973). The birds were given SAFRING (South African Bird Ringing Unit) age codes: chicks (1), juveniles (2), immature birds between 6 and 12 months (6), immature birds in general (3), or adults (4). Though the term 'immature' generally refers to the specific age class of 6, in this paper we use it to refer to all individuals younger than adults. **Table 1:** Numbers of adult and immature Kittlitz's Plovers captured for the first time (*N* captured) and their recaptures (*N* recaptures) during each collection period that were used to estimate the population size at the main ringing locations in Barberspan Bird Sanctuary (see Figure 1) between March 2009 and May 2010.

Location/ collection period	Ac	dults	Immatures		
	N	N	Ν	N	
	captured	recaptures	captured	recaptures	
Goose Point					
24–31 Mar 2009	28	7	21	10	
4–13 Oct 2009	50	8	-	-	
17–29 Oct 2009	77	18	-	_	
4–29 Oct 2009	-	_	12	2	
27 Jan–3 Feb 2010	16	1	23	2	
6–16 Mar 2010	21	13	55	5	
19–27 Apr 2010	44	13	11	4	
Sandy Beach					
3–5 Mar 2010	13	2	18	2	
27 Apr-1 May 2010	57	4	19	2	

#### Population size estimation

We estimated the size of the Kittlitz's Plover population in each of eight periods of intensive sampling between 24 March 2009 and 1 May 2010 (Table 1). We assembled all captures and recaptures of birds during each sample period and analysed them with a Bayesian model for estimating a population size, assumed to be constant during the sampling period (Underhill and Fraser 1989). Each sampling period was 3–12 d of continuous catching effort at a site. For immature birds we combined two sampling periods in October 2009 at Goose Point into one 23-day period because of small sample sizes (Table 1). We investigated the sensitivity of our population estimates to the length of the sampling periods.

We estimated the population sizes of adult and immature Kittlitz's Plovers separately for each sampling period, and also estimated the combined population size of adults and immature birds. Population size could only be estimated in sampling periods that included recaptures. The Underhill-Fraser (1989) method requires a string of 0s and 1s describing the sequence of first captures (denoted 0) and recaptures (denoted 1) during each sampling period. We used only one daily recapture of an individual in the string, to avoid bias by territorial 'trap-happy' individuals.

The model of Underhill and Fraser (1989) is based on applying Bayes Theorem to each successive capture of a bird and using this to update the probability distribution. The initial prior probability distribution is derived from an estimate of the maximum population size (Underhill and Fraser 1989). We set this at 2.5 times the number of different birds caught during a sampling period. We used an uninformative prior, so that each value between one and the estimated maximum population size was deemed equally likely. For each consecutive capture we obtained the distribution of posterior probabilities using the formulae of Underhill and Fraser (1989). There are two updating formulae: one if the bird captured is a first capture and another for a recapture. These posterior probabilities depend on the prior distribution at the previous catch. The mode (maximum probability) of a distribution of posterior

probabilities at each catch indicates the most likely population size. The posterior distributions tend to become more peaked and more stable as the number of captures increases. We also calculated the means, medians and 95% confidence intervals for each population estimate for adults, immature birds and both age groups combined for each collection period. At each iteration, the posterior distribution from the previous capture becomes the prior distribution for the following one. According to Underhill and Fraser (1989), the mode, mean and median of the population estimates should each become stable, helping to choose the best population estimate. Contrary to the examples presented by Underhill and Fraser (1989), we found the estimated mean and median population sizes were sensitive to the initial choice of maximum population size, but that the mode was relatively independent of this initial value. Thus we chose the mode of the probability distribution as the most consistent indicator of the estimated population size.

### Morphometric comparisons

To examine whether we could distinguish between local and immigrant populations we compared measurements of Kittlitz's Plovers caught at Goose Point and Sandy Beach in March and April 2010, separately for adults and immature birds. We used the Mann-Whitney test to compare their fat scores, and two-sample *t*-tests for comparisons of all the remaining measurements. We used only the measurements of birds at their first capture during a collection period for these morphometric analyses.

#### Movements

To describe the movement patterns of Kittlitz's Plovers, we mapped the movements of birds ringed at one location and recovered at another in the reserve between February 2008 and May 2010 (Figure 1). We checked the SAFRING database to determine if any of the 701 Kittlitz's Plovers ringed at Barberspan Bird Sanctuary since 2006 had been captured elsewhere.

# Results

# Population estimates

The largest estimated population size of adult Kittlitz's Plovers at Goose Point was in October 2009, with similar modes to the final posterior distribution for both collection periods that month at 140 adults (95% confidence interval 89-196) and 137 adults (95% CI 102-194), respectively (Figure 2). The modal estimate of the number of adults at Goose Point when the two October 2009 collection periods were combined was 161 individuals (95% CI 132-217). The smallest numbers of adults at Goose Point occurred in March 2009 and March 2010, estimated at 44 (95% CI 29-68) and 35 individuals (95% CI 22-69), respectively. The estimated sizes of the adult population were similar at Sandy Beach and Goose Point during March 2010, but in April 2010 the estimate was almost seven-fold larger at Sandy Beach, but at Goose Point it remained close to the level in March (Figure 2).

The largest estimated population size of immature birds at Goose Point was 119 birds (95% CI 49–140) in January–February 2010 (Figure 2). The estimated numbers



**Figure 2:** Population size estimates for adults (top), immatures (middle), and combined age groups (bottom) at Barberspan Bird Sanctuary. Symbols show the mode of the estimated population size (the population size with the highest probability, see text) at Goose Point (squares) and Sandy Beach (circles); whiskers represent 95% confidence intervals of the population estimates. Black horizontal bars on the *x*-axis indicate the length of collection periods: for exact dates see Table 1

of immature birds at Goose Point were smallest in March 2009 and April 2010: 13 birds (95% Cl 11–26), and 10 birds (95% Cl 7–48), respectively. In March 2010 and April 2010 the estimated populations of immature birds were larger at Sandy Beach than at Goose Point (Figure 2). The estimates for the total population size, based on combined captures of adults and immature birds at each location and collection period, corresponded closely with the sum of the estimated adult and immature population sizes (Figure 2).

#### Local recaptures

Of the 491 Kittlitz's Plovers that we caught at Barberspan Bird Sanctuary between February 2008 and April 2010, we recaptured 85 individuals at least once. Of these, 59% were recaptured, often multiple times, only at the location where they were ringed, both within and across different collection periods. For example, an adult Kittlitz's Plover ringed on 10 March 2010 at Goose Point was recaptured 14 times during March and April 2010 at the same location. Another Kittlitz's Plover ringed on 9 September 2009 at Godwit Bay was later recaptured 12 times at Goose Point during all collection periods between October 2009 and April 2010.

Of the 274 individuals captured at Goose Point, 7% were recaptured within 1 and 10 d of the first capture and 15% within 11 and 396 d of the first capture. Twelve of these birds were ringed and recaptured multiple times at Goose Point between September–October 2009 and March–April 2010, and 13 birds were encountered multiple times in March–April 2009 and in March–April 2010.

Regular ringing took place at Sandy Beach only in February 2008, March 2010 and April 2010, which limits comparisons with Goose Point. Of the 115 Kittlitz's Plovers captured at Sandy Beach, 5% were recaptured within 1 to 10 d of first capture, and one bird was ringed on 2 March 2010 and recaptured after 58 d on 29 April 2010.

#### Movements between localities

Thirty-five of the Kittlitz's Plovers that we ringed were recaptured around the perimeter of Barberspan at locations different from the ringing site. Some of these birds were recaptured several times at different locations, so we recorded altogether 44 movements within the reserve (Figure 1). Some individuals were observed at several ringing locations in the sanctuary. For example, a Kittlitz's Plover ringed at Goose Point on 29 March 2009 was recaptured at Godwit Bay on 14 September 2009, at Botany Bay on 20 September 2009 and at Goose Point again on 17 October 2009. None of the Kittlitz's Plovers ringed at Barberspan Bird Sanctuary had been recorded outside the reserve and no individuals ringed elsewhere were recorded there (SAFRING database, 9 May 2011).

# Morphometric comparisons, body mass and fat scores

To verify the hypothesis of a seasonal influx of birds from outside the reserve, which was suggested by the increased numbers of Kittlitz's Plovers between March 2010 and April 2010 at Sandy Beach (Figure 2), we compared the biometrics, body mass and fat scores of Kittlitz's Plovers caught at Goose Point and at Sandy Beach during these months.

Adults caught at Goose Point and at Sandy Beach in March did not differ in most measurements (Table 2). The mean bill and wing lengths of adults caught at Goose Point were significantly larger than of those caught at Sandy Beach in April (Table 2). Adults at Sandy Beach were on average 1.0 g heavier than adults at Goose Point in March ( $t_{65} = -2.84$ , p = 0.006) and 2.6 g heavier in April ( $t_{81} = -4.48$ ; p < 0.001) (Figure 3). Adults caught at Sandy Beach had significantly higher fat scores than adults at Goose Point in April (Mann-Whitney test: Z = 3.29, p = 0.001). The adults caught at Sandy Beach in March on average also

Month/measurement	Goose Point		Sandy Beach		<i>t</i> -test	
	Mean (SD)	N	Mean (SD)	N	t	р
March						
Head length (mm)	41.63 (0.847)	10	41.10 (1.093)	13	1.27	0.2194
Bill length (mm)	16.31 (0.737)	10	16.18 (0.877)	13	0.36	0.7199
Tarsus length (mm)	31.73 (0.933)	10	31.58 (1.301)	13	0.30	0.7685
Tarsus+toe length (mm)	53.0 (2.00)	10	51.3 (1.93)	13	2.05	0.0529
Wing length (mm)	107.9 (1.73)	8	106.4 (2.20)	8	1.52	0.1515
April						
Head length (mm)	41.08 (0.883)	26	41.07 (0.932)	52	0.02	0.9861
Bill length (mm)	15.99 (0.825)	26	15.59 (0.731)	52	2.16	0.0338
Tarsus length (mm)	31.72 (1.403)	23	31.82 (1.135)	52	-0.31	0.7605
Tarsus+toe length (mm)	51.9 (1.83)	26	52.2 (1.83)	52	-0.88	0.3825
Wing length (mm)	109.3 (2.66)	25	107.9 (2.48)	52	2.35	0.0212

**Table 2:** Comparison of measurements of adult Kittlitz's Plovers caught in March and April 2010 (dates of collection periods are given in Table 1) at two locations within Barberspan Bird Sanctuary. Results of *t*-tests are provided: *t* and *p* values, significant *p* values (p < 0.05) are highlighted in bold, marginally significant (0.05 ) are highlighted in bold italics



**Figure 3:** Mean body mass (top figure) and median fat scores (bottom figure) for adults in March and April 2010 at Sandy Beach (white bars) and Goose Point (black bars) at Barberspan Bird Sanctuary. In the top figure squares show means, bars represent standard deviations; in the bottom figure squares show medians, bars represent quartiles. Whiskers represent minimum and maximum values, values above whiskers show the numbers of birds captured in each collection period. Horizontal lines indicate significant differences: top figure – *t*-test, bottom figure – Mann-Whitney test, \* denotes p < 0.05, \*\* denotes p < 0.01, \*\*\*

had higher fat scores than those at Goose Point in April (Mann-Whitney test: Z = 2.34, p = 0.019) (Figure 3).

Immature birds caught in March at Goose Point had marginally but statistically significant longer tarsus-andtoe than those at Sandy Beach; this difference can be disregarded given the number of statistical tests performed (Table 3). Immature birds at Sandy Beach in April were 2.5g heavier than at the same location in March (t-test:  $t_{31} = -2.044$ , p = 0.049) and at Goose Point in March (*t*-test:  $t_{57} = -4.12$ , p < 0.001); the difference of 1.6 g with Goose Point in April was not significant (Figure 4). Immature birds at Sandy Beach in March had higher fat scores than those at Goose Point in March (Mann-Whitney test: U = 167.0; p = 0.002) and in April 2010 (Mann-Whitney test: U = 24.5; p = 0.028; Figure 4). The median fat score of immature birds at Sandy Beach in April 2010 was one score higher than at Goose Point in March 2010 (Mann-Whitney test: U = 211.0; p = 0.019, Figure 4).

#### Moult

We compared the stage of primary moult of adults at Goose Point with those at Sandy Beach in March and April 2010. In March 47% of adults caught at Goose Point and 62% of birds caught at Sandy Beach had new primaries, about 40% at both sites were caught during primary moult, and two birds at Goose Point and none at Sandy Beach still had old worn primaries (Figure 5). In April at Goose Point the proportion of adults with all new primaries increased to 87%, but at Sandy Beach in April the proportion of adults with new primaries decreased to 44%, which was lower than in March at the same site, and birds with old worn primaries predominated (Figure 5). This difference in the proportions of birds with new and old feathers was significant (chi-squared test with Yates' correction:  $\chi^2 = 16.14$ , p < 0.001).

# Discussion

The use of a Bayesian model to estimate population size Our method of estimating population size differed from that of Underhill and Fraser (1989) in that we chose to use the mode of the posterior probability distributions as an indicator of the most likely population size at each capture rather than **Table 3:** Comparison of measurements of immature Kittlitz's Plovers (SAFRING age categories 3 and 6 combined) caught in March and April 2010 (dates of collection periods are given in Table 1) at two locations within Barberspan Bird Sanctuary. Results of *t*-tests are provided: *t* and *p* values, significant *p* values are highlighted in bold

Month/measurement	Goose Point		Sandy Beach		<i>t</i> -test	
	Mean (SD)	N	Mean (SD)	N	t	р
March						
Head length (mm)	40.90 (1.24)	39	40.88 (0.77)	17	0.41	0.69
Bill length (mm)	16.44 (0.99)	39	15.10 (0.66)	17	1.46	0.15
Tarsus length (mm)	31.66 (1.55)	39	31.56 (0.99)	17	0.29	0.77
Tarsus+toe length (mm)	52.1 (2.1)	39	51.0 (1.2)	17	2.05	0.046
Wing length (mm)	104.8 (5.1)	32	106.4 (1.9)	13	-1.12	0.27
April						
Head length (mm)	41.02 (0.73)	6	41.04 (0.77)	14	-0.05	0.96
Bill length (mm)	16.22 (0.69)	6	15.66 (0.72)	14	1.69	0.11
Tarsus length (mm)	32.03 (0.97)	6	31.34 (1.55)	14	1.05	0.31
Tarsus+toe length (mm)	52.2 (1.3)	6	51.6 (1.7)	14	0.74	0.47
Wing length (mm)	106.8 (4.3)	6	106.3 (2.6)	14	0.35	0.73



**Figure 4:** Mean body mass (top figure) and median fat scores (bottom figure) for immature birds in March and April 2010 at Sandy Beach (white bars) and Goose Point (black bars) at Barberspan Bird Sanctuary. In the top figure squares show means, bars represent SD; in the bottom figure squares show medians, bars represent quartiles. Whiskers represent minimum and maximum values, values above whiskers show the numbers of birds captured in each collection period. Horizontal lines indicate significant differences between groups: top figure – *t*-test; bottom figure – Mann-Whitney test; \* *p* < 0.05, \*\* *p* < 0.01, \*\*\* *p* < 0.001



**Figure 5:** Proportion of birds with old primaries (black bars), in active moult (grey bars) and with new primaries (white bars) of adult Kittlitz's Plovers at their first capture in each collection period during March and April 2010 at two locations in Barberspan Bird Sanctuary. Sample sizes given above bars;  $\chi^2$  test for difference in proportions of birds with new and old feathers; \*\*\* p < 0.001

the mean or the median, which we found were sensitive to changes in the initial assessment of the maximum population size. In a few cases we found that if we assumed too small an initial population size the probability distributions were extremely right-skewed and the mode was at the maximum assumed population size. This indicated that a larger population size should have been used as the initial assessment. When we repeated the calculations after increasing the estimated population size by 50 individuals in several consecutive steps, the mode of the probability distribution suggested a consistent estimate of population size, despite subsequent increases in the assumed population size. In contrast, the median and the mean varied considerably among the calculations repeated with an increased population size. This was likely caused by the few recaptures in some collection periods, in contrast with the dataset analysed by Underhill and Fraser (1989), where after several days almost all the studied population of temporarily resident Malachite Sunbirds *Nectarinia famosa* had been ringed and there was a large probability of a recaptured bird in each next catch. Thus we recommend using the mode in applications of the method of Underhill and Fraser (1989) to data sets that deviate from their ideal experimental situation and contain a low proportion of recaptures.

The estimates obtained using combined datasets of adults and immature birds from a collection period were consistent with the sum of the population sizes estimated separately for adults and immature birds (Figure 2). The population estimates for adults from two collection periods in October were close and the estimate we obtained when we combined both October collection periods as one sample was also similar. This suggests that the estimates are not substantially biased by the different length of the collection periods and that this method of estimating populations produces consistent results.

#### Breeding patterns of Kittlitz's Plovers

Our results showed that the estimated population size of adult Kittlitz's Plovers at Goose Point reached its maximum in October 2009 (Figure 2). This likely coincided with their breeding season. We observed Kittlitz's Plovers in breeding plumage between September 2009 and April 2010, and in October 2009 we trapped chicks and juveniles as well as several females about to lay eggs at Goose Point and at Godwit Bay (Meissner et al. 2011). This corresponds with past accounts, such as Milstein (1975) who observed a peak in Kittlitz's Plover breeding activity in October-November and Tarboton et al. (1987) who found that the eggs in 72% of nests at Barberspan Bird Sanctuary were laid between August and November. However, Farkas (1962) noted that the 'most prolific breeding' occurs in Barberspan Bird Sanctuary during the autumn and winter months (March-July), when the overall numbers of Kittlitz's Plovers peak at the reserve. Although we did not observe large numbers of breeding birds between March and July, we did notice a few unhatched eggs and chicks in March and April 2010 at Goose Point.

There are possible explanations for these contradictions about timing of breeding of Kittlitz's Plovers at Barberspan Bird Sanctuary. The breeding season for this species varies between climates and habitats, and over most of its range breeding extends across more than half a year (Turpie and Tree 2005). Annual variation in rainfall and temperature modifies the timing of breeding between years at a location and this phenomenon has been described at Barberspan Bird Sanctuary (Milstein 1975). Another hypothesis is that resident Kittlitz's Plovers have two or three consecutive broods, thus extending the breeding season. Repeated clutches by one pair of Kittlitz's Plovers have not been recorded in the wild, but Tree (1974) at Lake McIlwaine in Zimbabwe observed a female that produced two clutches of eggs, neither of which was successful, in July and August, with different males. In captivity a female was observed to lay a second clutch while the male tended the chicks from the first brood (Urban 1986). Multiple recaptures of individual adult Kittlitz's Plovers at Goose Point in two

consecutive breeding seasons and during the period in between suggest that these birds are local residents, and they might lay more than one clutch at the same location over the extended breeding season. Consistent estimates for adult Kittlitz's Plovers at about 40 individuals in March 2009 and March 2010 suggest that this might be the minimum population size of local residents at Goose Point over the whole breeding season. Adults that have bred successfully in earlier months could have left Goose Point by March for another location in the reserve, as suggested by movements around the perimeter of Barberspan (Figure 1), or for other destinations.

Assuming that Kittlitz's Plovers begin breeding at Barberspan Bird Sanctuary in September and peak in October, their offspring should first be observed three to five weeks later. It takes 22-30 d for a breeding pair to incubate eggs and 25-32 d for the hatchlings to fledge (Tree 1974, Turpie and Tree 2005). The immature population peaked at Goose Point at the turn of January and February 2010, about two to three months after the peak of the adult numbers in October 2009 (Figure 2). Most (75%, n = 17) of the immature birds caught in January– February 2010 were aged as 0-6 months old. They did not form flocks, but were dispersed over Goose Point. Thus we assume that these immature birds were derived from the local hatchlings. An average clutch size of 1.9 eggs per breeding pair was described by Tjørve et al. (2008) in the Western Cape. If we compare the peak numbers of adults and immature birds estimated at Goose Point (Figure 2), this gives 1.5 immature offspring per pair of adults, which corresponds with these results.

## Spatial and behavioural segregation of Kittlitz's Plovers

The large increase in the numbers of adult Kittlitz's Plovers that we observed at Sandy Beach from March to April 2010 corresponded to the observations of winter influxes of this species to Barberspan Bird Sanctuary (Farkas 1962, Milstein 1975). Farkas (1962) might have confused these irregular high numbers of Kittlitz's Plovers during the autumn and winter months as the peak of the breeding period. These birds might be long-distance migrants or nomads that arrive at Barberspan, as well as birds from the reserve and surrounding areas gathering at ideal feeding locations in the reserve after breeding, or a mixture of these categories. We did not observe such concentrations of Kittliz's Plovers earlier in the season at Barberspan Bird Sanctuary. It is noteworthy that immature birds formed only a small proportion of birds caught at Sandy Beach in April 2010 in contrast with March 2010 (Table 1). This shows that the influx was formed mostly of adults, or of immature birds that had already moulted into adult plumage. It is difficult to distinguish between resident and itinerant populations, because they tend to mix at the same locations (Tree 2001).

Adults caught at Sandy Beach in April 2010 were on average heavier and fatter than those caught at Goose Point in April and at both locations in March (Figure 3). This suggests that the flocks we observed at Sandy Beach in April were mostly recently arrived itinerants, with fat reserves allowing for further movements. Another possibility is that the birds at Sandy Beach were fatter because more food was available there. At Sandy Beach in April 2010 we observed flocks of Kittlitz's Plovers arriving shortly after daylight that immediately started to feed on wet beaches or damp patches of medium-height grass with abundant insects. We did not observe similar behaviour at Goose Point, where the birds were more dispersed in the dry parts of the peninsula covered with sparse short grass, which is their preferred breeding habitat (Tree 1974, Urban 1986, our own observations). However, in April we observed flocks of 50-100 Kittlitz's Plovers flying in at evenings to the base of the Goose Point peninsula or to the nearby Peters' Pan. Our recaptures of birds moving around the reserve did not document these movements, probably because the flocks of Kittlitz's Plovers congregating immediately behind Goose Point stayed outside the range of our traps and nets, and the flocking birds tended not to mix with the territorial 'residents'. Intraspecific spatial and habitat segregation between residents and arriving migrants has been described in passerines (e.g. Pérez-Tris and Tellería 2002, Tellería & Pérez-Tris 2004) and in waders (Colwell and Oring 1988). Colwell and Oring (1988) showed that at intra- and inter-specific levels breeding waders preferred terrestrial microhabitats, and migrants used wetter feeding microhabitats at an inland lake in Saskatchewan, Canada. This corresponds with our observations of the dispersal and flocking of Kittlitz's Plovers.

The biometric differences in bill and wing length between the adult Kittlitz's Plovers caught at Sandy Beach and at Goose Point in April suggested that these birds might come from different populations (Table 2). This is supported by the occurrence at Sandy Beach in April of a group of adults with old primaries, which had not been observed there a month earlier (Figure 5). At Goose Point the proportion of birds with new feathers increased between March and April 2010 (Figure 5), probably as a consequence of resident birds finishing the moult that was in progress a month earlier. Kittlitz's Plovers moult their primaries after they finish breeding (Urban 1986, Turpie and Tree 2005, our own observations), but migrant waders often do not moult their primaries before they migrate and replace them only when they reach staging areas rich in food (Prater 1981, Ginn and Melville 1983).

The higher proportion of birds with old primaries at Sandy Beach might explain why birds caught there had on average 1.5 mm shorter wing lengths in comparison with those from Goose Point (Table 2). This corresponds with the results of Meissner et al. (2011), which showed that the wing lengths of Kittlitz's Plovers caught at Barberspan Bird Sanctuary decreased 2 mm on average during two months (September–October 2009) due to primary feather wear. Birds with old feathers in April could include local residents that had finished breeding a few months earlier and had replaced their primaries, which had by then become worn.

Our results suggested an influx of Kittlitz's Plovers from outside Barberspan Bird Sanctuary in April, but we have no clue about the origin of these birds. All our ringing recoveries were from Kittlitz's Plovers previously ringed within our study area. The SAFRING database did not contain any records of movements of Kittlitz's Plovers to other localities. Breeding populations of Kittlitz's Plovers at sites north of Barberspan Bird Sanctuary, in Botswana, Zimbabwe and Zambia, are migratory, and after breeding are thought to move southwards to the inland and coastal areas of South Africa (Tree 2001, Turpie and Tree 2005, Dodman and Parker 2009). These movements are irregular, depending on local rainfall (Tree 2001, Turpie and Tree 2005). Barberspan Bird Sanctuary is located along the potential migration route. Winter influxes of Kittlitz's Plovers here are irregular, occurring only in some years (Farkas 1962, Milstein 1975). This suggests that the study area can temporarily hold migrant populations of Kittlitz's Plovers. Nomadic movements of Kittlitz's Plovers over short distances have also been described (Underhill et al. 1999), as well as local movements of waders to the perennial Barberspan lake from large numbers of temporary pans which dry up after the rainy season (Milstein 1975).

In conclusion, we observed spatial segregation between resident, breeding Kittlitz's Plovers and the non-breeding flocks. It is likely that we observed an influx of Kittlitz's Plovers at Barberspan Bird Sanctuary in April 2010 that differed from the local population in the wear of primaries and bill length, and which formed feeding flocks of non-breeding birds that might have included local non-breeders. It remains unclear whether the newly arrived birds were nomads that came from the adjacent regions or migrants from farther away. Unraveling this riddle would need intensive ringing or a colour-marking study conducted in parallel within the reserve and outside. Our study also demonstrated that that Barberspan Bird Sanctuary still experiences the same seasonal fluctuations in the numbers of Kittlitz's Plovers that were observed more than 40 years ago.

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