



Original Article

Adult sex ratio and operational sex ratio exhibit different temporal dynamics in the wild

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Adult sex ratio (ASR, the proportion of adult males in the adult population) and operational sex ratio (OSR, the proportion of sexually active males in the mating pool) are fundamental properties of breeding populations and they are often linked to mating systems and sexual selection. However, ASR and OSR emerge via different routes in a population and may exhibit different temporal patterns. Here, we use data from a well-monitored polygamous snowy plover *Charadrius nivosus* population sampled over 3 consecutive breeding seasons to investigate whether temporal changes in ASR relate to changes in OSR. We found that snowy plovers exhibited male-biased ASR and OSR. Consistent with theoretical expectations, OSR was more variable than ASR. However, there was no consistent relationship between OSR and ASR: in only 1 of the 3 study years we found a weak positive relationship ($r = 0.22$). The lack of association was corroborated by time series analyses and sensitivity tests. Our work therefore suggests that ASR and OSR exhibit different temporal patterns in a polygamous population, and we call for further theoretical and empirical studies that analyze their relationship across a range of different breeding systems.

Key words: adult sex ratio, mating system, operational sex ratio, social environment, temporal variation, within-season variation.

INTRODUCTION

Sex ratios are fundamental demographic properties of populations that are tightly linked to population growth (Bessa-Gomes et al. 2004; Donald 2007; Veran and Beissinger 2009), mating systems, parental behavior (McNamara et al. 2000; Székely et al. 2000; Kokko and Jennions 2008; Liker et al. 2014), and sexual selection (Emlen and Oring 1977; Clutton-Brock and Vincent 1991;

Kvarnemo et al. 1995; Kvarnemo and Ahnesjö 1996; Shuster and Wade 2003; Silva et al. 2010). Sex ratios can be measured at several stages of development: at conception (primary), birth (secondary), and during adult life (adult sex ratio [ASR] and operational sex ratio [OSR]). Theoretical and empirical studies have identified numerous ecological and evolutionary implications of sex ratios during adult life across several taxa on ecology, behavior, and life histories (Kokko and Jennions 2008; Veran and Beissinger 2009; Székely et al. 2014).

In nature, sex ratios are highly variable and could change dynamically through time in a population (Emlen and Oring 1977; Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992;

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Kvarnemo and Ahnesjö 1996; Forsgren et al. 2004). Nonetheless, studies that evaluate temporal variation in sex ratios are scarce (but see Pettersson et al. 2004; Arendt et al. 2014), and it is unknown whether the variability of sex ratios is a common trait of all populations or associated with certain species, mating system, or types of sex ratios.

Much attention has been paid to the demographic and life-history mechanisms that generate biases in ASR: 1) biases in early life sex ratios (i.e. at conception or at birth) (Fisher 1930; Wilson 1975); 2) sex-specific mortality of juveniles and/or adults (Clutton-Brock et al. 2002; Le Galliard et al. 2005); 3) sex differences in maturation times (Lovich and Gibbons 1990); 4) sex-specific migration and dispersal (Dale 2001; Clutton-Brock et al. 2002; Le Galliard et al. 2005; Steiffetten and Dale 2006); and 5) sex differences in arrival time to breeding grounds (Rubolini et al. 2004; Kokko et al. 2006). Attention to how ASR impacts on behavioral and reproductive traits has increased recently (Donald 2007; Kokko and Jennions 2008; Székely et al. 2014). For example, male-biased ASR can be related to intensified aggression toward females in lizards (Le Galliard et al. 2005), influence mating rates in invertebrates and mammals (DeLong 1978; Debuse et al. 1999; Karlsson et al. 2010), higher divorce rates in fish and birds (Beltran et al. 2009; Liker et al. 2014), and reversed sex roles in shorebirds (Liker et al. 2013).

Previous empirical and theoretical research on the importance of sex ratios for mating and parental care has focused primarily on OSR (Emlen and Oring 1977). For example, male-biased OSR is related to the development of sexual characters in insects (Pomfret and Knell 2008), loss of choosiness in male fish (Berglund 1994), intensified courtship behavior in fish (Forsgren et al. 2004; Silva et al. 2010), and higher female brood desertion rates in fish (Balshine-Earn and Earn 1998). Theory suggests that the degree of monopolization of mates may increase if OSR is biased toward one of the sexes leading to changes in the intensity of sexual selection within a population (Emlen and Oring 1977; Kokko and Jennions 2008; Jennions and Kokko 2010). OSR emerges as a combination of variation in ASR plus the behavioral and mating decisions of individuals. As males and females in the adult population shift between sexually active and inactive periods dynamically (time-in and time-out, respectively) (Clutton-Brock and Parker 1992; Székely et al. 2000; Alonzo 2010), OSR is expected to be more variable than ASR over time.

Predicting the relationship between OSR and ASR is not trivial. OSR and ASR may be tightly linked or correlated within a population, as the first is a subset of the latter and they have similar biological implications. But OSR and ASR are inherently different (Kokko and Jennions 2008; Székely et al. 2014) and hence may be uncorrelated, given that OSR may be more dynamic than ASR as it depends on the behavioral and mating decisions of individuals. A few studies have quantified and reported both OSR and ASR in wild populations at the same time (Whitfield 1990; Mitani et al. 1996; Gerber 2006; Veran and Beissinger 2009; Chak et al. 2015). Nonetheless whether they are correlated with each other has not been formally tested. Although ASR and OSR may be different from each other and may not be correlated, several experimental studies use the concepts of OSR and ASR interchangeably (reviewed by Kokko and Jennions 2008), perhaps because during initial experimental conditions when all individuals are unmated OSR will equal ASR if all the individuals involved are sexually active. Nevertheless, as the experiment progresses and individuals are allowed to interact, ASR will remain stable, whereas OSR will inevitably change as some individuals mate and are in time-out and

others reenter the mating pool (Kvarnemo and Merilaita 2006). ASR and OSR can only be identical or highly correlated, if periods of sexual activity are exactly the same or very similar in males and females, a condition that is rarely met in nature (Székely et al. 2014). Understanding the temporal relationship between ASR and OSR is an important precursor to understand the dynamics of mating competition and parental care.

We had 2 objectives in this study: first, to investigate the temporal variation of ASR and OSR and second, to examine the correlation between ASR and OSR in a wild polygamous population. We studied the temporal variation in both ASR and OSR in a population of snowy plovers *Charadrius nivosus* (Küpper et al. 2009) breeding at Bahía de Ceuta, Mexico. This shorebird is suitable for exploring sex ratio variation for 3 reasons. First, snowy plovers are partial migrants; some spend only a part of the breeding season at the breeding site, whereas others remain in the area all year (Küpper C and Cruz-López M, unpublished data). Therefore, the date of arrival and departure to/from the breeding site may vary considerably between individuals, giving rise to temporal fluctuations in the number of adult males and females in the local population. Second, snowy plovers have variable breeding behavior: both sexes incubate (Vincze et al. 2013) but after hatching, the female (or rarely the male) may abandon the brood. The remaining parent stays with the chicks until fledging. However, both parents often stay together until the offspring fledge (Warriner et al. 1986; Page et al. 2009). Third, snowy plovers are sequentially polygamous and often have multiple mates in one breeding season. Deserting parents attempt to quickly remate and start a new breeding attempt (Warriner et al. 1986; Beamonte-Barrientos et al. unpublished data). The caring parent may also renege with a new mate after successfully fledging the young. Taken together, the partial migratory behavior and the complex mating system of snowy plovers may interact with both ASR and OSR. Because of the predominance of polyandry and male brood care in snowy plover populations, we predicted an overall male-biased ASR and OSR (Liker et al., 2013). We anticipated that OSR would have greater variation than ASR because it should change more dynamically over the breeding season than ASR, given that females normally abandon the broods and remate entering and exiting the breeding pool more frequently than males. Finally, because ASR and OSR have different dynamics and are influenced by different population parameters, we predicted that both indices are not correlated over time.

METHODS

General fieldwork procedures

Fieldwork was carried out at Bahía de Ceuta, Sinaloa, Mexico (23° 54'N, 106° 57'W) during the snowy plover breeding season (April to July) from 2006 until 2011. Bahía de Ceuta is a wetland complex (1497 ha) located at the Gulf of California, consisting of swamps, natural salt marshes, and mangrove forests (Nava 2007). The study area, a salt marsh surrounding several abandoned salt evaporation ponds, covers approximately 150 ha. Every year since 2006, this snowy plover population has been intensively monitored during the breeding season and typically 30–100 adult snowy plovers breed at the site (Carmona-Isunza et al. 2015).

We followed basic fieldwork methodology described in detail in Székely T, Kosztolányi A, Küpper C (unpublished report). We searched for nests by identifying incubating adults from a distance of 100–200 m using a mobile hide. We checked nests every

3–5 days to monitor clutch survival. We considered laying date as the date when the clutch was completed and parents started to incubate the eggs persistently. If a nest with a complete clutch was found, we estimated clutch completion date by floating eggs in water when the nest failed (the density of eggs decreases progressively as they lose water during incubation) or from observed hatching dates assuming an incubation period of 25 days (Székely T, Kosztolányi A, Küpper C, unpublished report). We captured adults on the nest using funnel traps and marked them with a metal ring and with individual color ring combinations (518 adults from 2006 until 2011). Around the expected hatching date, we checked nests daily in order to ring chicks before they left the vicinity of the nest. In addition to the metal ring, we marked chicks with a single color ring to help identification in the field. Some families were only encountered for the first time after the chicks had left the nest. For those families, we estimated chick age and hatching date (and thereafter laying date) using the tarsus length of chicks, assuming linear growth (Dos Remedios et al. 2015). We considered a brood as fledged and independent when the oldest chick had reached the age of 25 days (Székely and Cuthill 1999).

We recorded the number of chicks and the sex of the attending parent(s) immediately after chicks hatched and repeated these observations every 2–4 days until the brood had perished or fledged. When only one parent was present, we observed the focal brood for at least 15 min or until the missing parent was seen. This allowed us to make sure that missing parents were not hiding or only temporarily absent. If the same parent was absent during 2 encounters in a row (without reappearing in subsequent observations), we considered the parent as having abandoned the brood. Additionally, we recorded the identity and sex of every ringed individual that was resighted throughout the breeding season using a spotting scope or binoculars, noting the date, time, and location.

Population surveys

We carried out population surveys every 2 weeks during the breeding season and once a month or every 2 months outside of the breeding season during 2009, 2010, and 2011. During each survey, observers moved slowly with a mobile hide through the entire study area and stopped every 100–200 m to record color-ringed plovers, the number of unmarked plovers and the sex of each adult (ringed or unmarked). Sexes were identified according to the dimorphic plumage present during the breeding season: plover males have darker head and breast bands than females (Argüelles-Ticó et al. 2015) and confirmed by molecular sexing (details in Dos Remedios et al. 2015). All color ring combinations recorded on each survey were subsequently checked using the record of color ring combinations used in this population; observations with incomplete or inexistent ring combinations were considered erroneous readings and were not used in the analyses. This is justified, because color ringing of snowy plovers at other locations nearby (<2000 km) started only in 2010, and only 1 individual ringed elsewhere was observed in 2012 among a total of 1678 sightings of color-ringed individuals since 2009 (Küpper C and Cruz-López M, unpublished data). Therefore, the chances of encountering a ringed individual from another location are small. In 23 (0.014%) cases, the sex of ringed individuals recorded during surveys did not match the sex registered on previous captures; in these few cases, the sex recorded during surveys was replaced with the presumably correct previously determined sex when available.

Estimating individual presence intervals

Not all snowy plovers remain at the breeding site throughout the entire breeding season. Breeding dispersal is high and males and females may nest at different locations hundreds of kilometers apart (Stenzel et al. 1994). Therefore, we estimated the presence intervals of individuals (periods of time when individuals were present) in the population during each breeding season based on information from nesting, family observations, and presence in surveys. We defined the start of a breeding season as 10 days before the first laying date recorded in the study site each year, midpoint of the 8–11 days it took individuals to bond with a partner and establish a nesting territory (see Estimating time-out periods). We considered a breeding season finished 25 days after the last brood hatched in the population each year, the minimum time in which plover chicks fledged (normally 25–30 days after hatching, Székely and Cuthill 1999). We used records from breeding season surveys and nonbreeding season surveys that were conducted a maximum of 30 days before the start or after the end of the breeding season, opportunistic resightings, nest and brood checking to determine the day when each individual was first seen (hereafter “arrival date”), and the day when it was last seen (hereafter “departure date,” see e.g. Fig. 1a). We assumed that each individual remained at the study site for the entire presence interval delimited by its arrival and departure date.

Estimating ASR

ASR estimates were based on presence intervals of a sample of breeding adults. Our sample consisted of 111 ringed adults (in 2009, 2010, and 2011, males: 46, 38, and 24; females: 27, 32, and 21, respectively) that bred in at least one of the 3 years of the study and were individually ringed at least 1 year before the focal year (i.e. known individuals). Ringing takes place during incubation and breeders ringed in a focal year would have been recorded in surveys or resightings only after their ringing date. The sample used represented the 71% (2009), 54% (2010), and 48% (2011) of the total number of ringed breeders each year, and we only calculated presence intervals for these known individuals. To estimate ASR at any given day of the breeding season, we counted the number of known males and females present that day (using the estimated presence intervals, see examples of this computation in Fig. 1b). ASR was computed as the number of males present divided by the total number of males and females present.

Estimating time-out periods

A time-out period is the time spent during pair-bonding and caring for eggs or chicks, i.e. when an individual is “out” of the breeding pool, following the definition of Clutton-Brock and Parker (1992). We calculated time-out periods for each reproductive event of each ringed individual; individuals were considered as available to breed (“time-in”) during the periods when they were not in time-out (Fig. 1a), i.e. the conditions are mutually exclusive. For each time-out period, we calculated its initial day (T_i) and final day (T_f). T_i was defined as the initial day of pair-bonding characterized by courtship, nest scraping, and/or copulation behavior. Actual dates when pair-bonding started were unknown, therefore T_i was estimated as the date when the last egg of the clutch was laid minus 10 days (Fig. 1a). We estimated this 10 day-period of pair-bonding using the mean time it took for renesting individuals to complete a new clutch (mean \pm SE: 9.37 ± 0.89 days, $n = 22$ males and 49 females that renested).

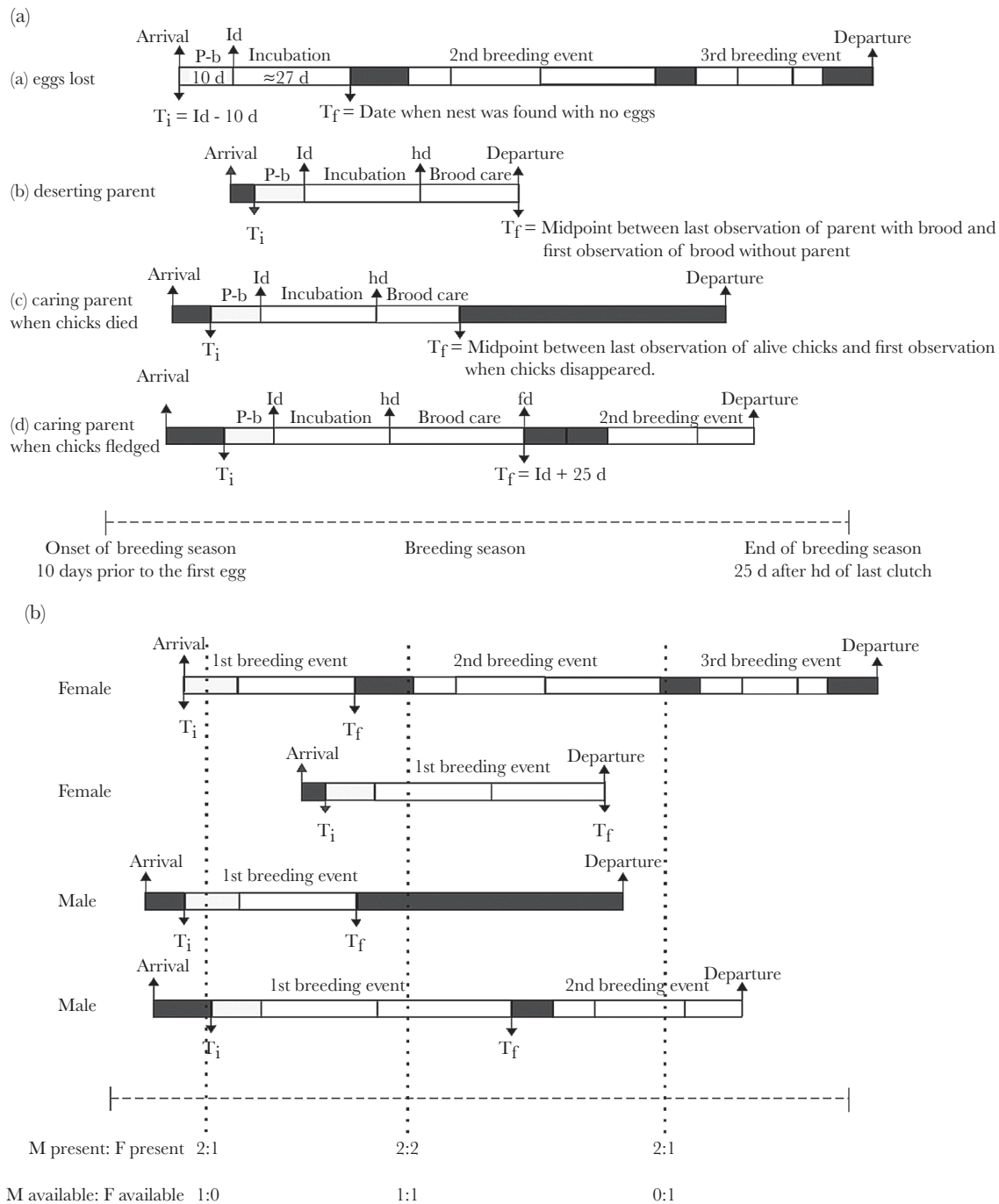


Figure 1

(a) Time-out periods (white boxes) of male and female snowy plovers for: (a) failed nesting attempts, (b) deserting parents, (c) caring parents when chicks died, and (d) caring parents when chicks fledged. Examples of arrival and departure dates are shown, and filled boxes represent examples of the period of time an individual was available to breed (time-in), ld stands for laying date, hd for hatching date, fd for fledging date, T_i is initial date of time-out, T_f is final date of time-out. Second and third breeding events may have occurred for some individuals as examples show, these events are split in three periods corresponding to pair-bonding time ($P-b$), incubation and brood care. (b) Example that shows how ASR and OSR were calculated. Vertical dotted lines represent example days for which the number of males (m) and females (f) were counted using the dates of arrival and departure and the estimated time-out periods.

T_f coincided with nest (or brood) failure or the termination of parental care. For failed nests (e.g. flooded, eggs predated or disappeared), T_f of males and females was considered to be the day when the nest was found with no eggs; when this information was not available, T_f was the date when the last egg of a failed clutch was laid (Fig. 1a [a]). For nests that produced at least one chick,

T_f depended on whether the parents deserted their broods and on chick survival. For a deserting parent, T_f was the midpoint between the last day the parent was seen caring for its brood and the first day it was absent (Fig. 1a [b]). For caring parents, T_f depended on chick survival in 2 aspects: 1) if all chicks died before fledging, T_f was the midpoint between the last date when the last surviving

chick was seen alive and the first day when the parent was seen without the chick(s) (Fig. 1a [c]); 2) if chick(s) fledged, T_f equalled the hatching date plus 25 days, the time required for the offspring to fledge and make the transition to independence (Székely and Cuthill, 1999) (Fig. 1a [d]). Whenever the survival of chicks was unknown, T_f was the last day when the family was seen, except for chicks that were still alive when fieldwork was concluded; in the latter case, chicks were considered to have fledged.

We assumed an individual was in the breeding pool whenever T_f from its last breeding event and T_i from the next breeding event did not overlap. This includes also cases when an individual did not switch mates because we reasoned that the opportunity to change mates existed.

Estimating OSR

To estimate OSR, we used the same sample of ringed adults used to estimate ASR (described in Estimating ASR). We counted the number of known males and females present that were available to breed (i.e. they were not in time-out, see examples of this computation in Fig. 1b) at any given day of the breeding season. Similar to ASR, OSR was computed as the number of males present and available to breed divided by the total number of males and females present and available to breed in our sample. For days when we could not compute OSR (i.e. division by 0 because all marked adults were unavailable for breeding, 6.6% of days all recorded in the beginning of the breeding season of 2011), we set OSR to 0 for analysis and omitted these records from the figures. Omitting these few cases from the analysis or replacing its value for the mean OSR did not change the results.

Statistical analyses

In order to describe temporal variation in ASR and OSR, we report time series plots showing daily estimates with their associated 95% confidence intervals (CIs) for proportions calculated using the Clopper and Pearson method (Clopper and Pearson 1934) and provide the estimated median and interquartile ranges of ASR and OSR per year. We used Levene's test (based on absolute deviations from the median) to compare variation between ASR and OSR.

Daily estimates of ASR and OSR (estimates for a total of 119 [2009], 131 [2010], and 115 days [2011]) are nonindependent data points obtained over a time interval; therefore, in order to test whether ASR and OSR were correlated, we performed a formal time series analysis that started by removing the trends of the series to avoid spurious correlations, as suggested by Box and Jenkins (Chatfield 2003). We carried out time series analyses separately for each year and for ASR and OSR. We removed the trends present in the series by using 1^o differentiation (i.e. computing differences between consecutive observations) (Chatfield 2003). We confirmed nonstationarity of differenced series using the unit root test but also used periodograms and autocorrelation plots to ensure the series were detrended. Despite the differentiation, the ASR estimates of 2011 and OSR estimates of 2009, still suffered from autocorrelation, thus, for these 2 series, autoregressive moving average models (ARIMA) were fitted applying the Box-Jenkins approach (Chatfield 2003). To cross-correlate ASR and OSR separately for each year and examine their association we used the differenced series and residuals from the ARIMA models to evaluate the non-autocorrelated part of each series, i.e. the stochastic term.

Cross-correlations allowed us to test the correlation of ASR and OSR on the same point in the time series (0 day lag, corresponding

to a Pearson correlation) but also the correlations for various time lags. We performed cross-correlations for -20 to 20 day lags to examine the potential lagged relationship between ASR and OSR. We only report cross-correlation coefficients for 0 day lag to describe the correlation between ASR and OSR on a same day, and cross-correlation coefficients for the peak cross-correlation observed in each year throughout all lags to evaluate potential cross-correlations in lagged series.

Sensitivity analysis

The estimation of ASR and OSR in this study was not computed from direct counts of males and females in a census; instead, it was derived from data on reproduction collected for each individual. The data of reproductive events are inherently based on simplified assumptions (e.g. chicks fledge after 25 days), estimations (e.g. chicks age calculated with tarsus and beak lengths), and field observations (e.g. color codes recorded by several observers) that introduced errors or variation that the method did not account for. We used 2 parameters to estimate ASR, arrival date and departure date (Table 1), whereas to estimate OSR, we used arrival date and departure date, plus 3 other parameters: laying date, 10 days of pair-bonding (to estimate T_i), and T_f (Table 1). Error or variation in these 5 parameters could potentially lead to spurious biases in ASR and OSR.

To explore how variation/error in these parameters could influence our baseline values of ASR, OSR, and their correlation, we carried out a sensitivity analysis in 3 steps. First, we modified each parameter of each individual by drawing a new date at random from a normal distribution having a mean equal to the original estimation of the parameter of that specific individual and a standard deviation of ± 1 day. Second, using the new dates of parameters generated for each individual, we estimated ASR and OSR newly, using only one of the modified parameters at a time. Parameter modification yielded 2 different estimations for ASR (Table 1 [a–b]) and 4 different estimations for OSR (Table 1 [a–d]). We also report an additional estimation for ASR and OSR in which all parameters were modified at the same time (Table 1 [e]). Finally, we ran time series analysis (as described above) with each new estimate of ASR and OSR and ran cross-correlations between all possible combinations of the different estimates of ASR and OSR.

Statistical analyses and plots were carried out using R (R Development Core Team 2015, Version 3.2.0). Time series analysis and cross-correlations (*crosscorr* in Econometrics Toolbox) were performed using Matlab (R2012b, The MathWorks Inc., Natick, MA, 2012).

RESULTS

Temporal variation in ASR and OSR

Both ASR and OSR tended to be male biased (ASR median = 0.64, 0.56, 0.60; OSR median = 0.75, 0.59, 0.75; $n = 119, 131, 115$ days in 2009, 2010, and 2011, respectively), although in daily estimates the majority of 95% CIs included 0.5 (Fig. 2). In general, CIs of OSR were larger than those for ASR. OSR interquartile ranges were substantially larger than those of ASR throughout the 3 years (interquartile ranges of ASR: 0.02, 0.05, and 0.09 and OSR: 0.13, 0.21, and 0.31 in years 2009, 2010, and 2011, respectively). Consistently, the variance in OSR was significantly more extensive than that of ASR (Levene's test: $F_{1,714} = 221.75, P < 0.01$).

Table 1
Definition of parameters used to estimate ASR and OSR in the analyses of snowy plover data

Parameter	Baseline parameters definition	Modified parameters per individual ^a	Sex ratio impacted	
			ASR	OSR
a) Arrival date	First time seen	First time seen \pm 1 day	✓	✓
b) Departure date	Last time seen	Last time seen \pm 1 day	✓	✓
c) T_i	Laying date minus 10 days of pair bonding	$T_i \pm$ 1 day	—	✓
d) T_f	T_f day when the nest was found with no eggs, parent deserted, chicks died or fledged	T_f of individual \pm 1 day	—	✓
e) All parameters modified at once		Arrival date of individual \pm 1 day, departure date of individual \pm 1 day, laying date of individual \pm 1 day, 10 days of pair bonding \pm 1 day, T_f of individual \pm 1 day	✓	✓

^a T_i is initial date of time-out and T_f is final date of time-out. The table also provides the parameter values we used in sensitivity analyses. Modified parameters were randomly drawn for each individual in our sample from a normal distribution with the mean \pm SD specified in the table.

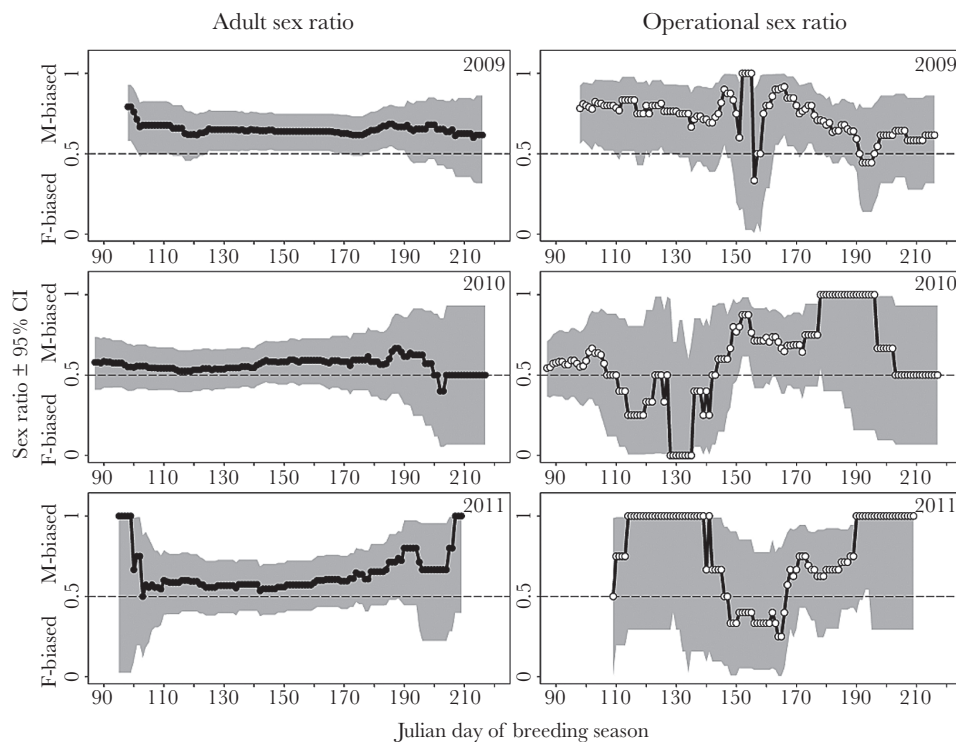


Figure 2

ASR (filled dots) and OSR (open dots) time series with 95% confidence intervals in snowy plovers breeding at Bahía de Ceuta, Mexico. Broken line demarks unbiased sex ratio (1:1). Julian day refers to the number of days since the 1st of January.

Does ASR predict OSR?

Same day correlations (0 day lag) of ASR and OSR varied each year. In 2009, it was negative but nonsignificant; in 2010, positive and significant; and in 2011, it was positive but nonsignificant (Table 2). These results were consistent with those derived by peak cross-correlations: the peak correlation in 2009 was nonsignificant (peak cross-correlation: $r = 0.13$, lag = -15 days, $P = 0.53$; Fig. 3). In 2010, the peak correlation corresponded to the 0 day lag, indicating that more male-biased ASRs were correlated with more male-biased OSRs instantaneously (peak cross-correlation: $r = 0.22$, lag = 0, $P = 0.01$; Table 2: Original ASR versus Original OSR, Fig. 3). Year 2011 showed a negative peak correlation ($r = -0.35$, lag = 9 days, $P = 0.001$; Fig. 3), i.e. male-biased ASRs were correlated with female-biased OSRs (and *vice versa*) 9 days later.

Sensitivity analyses

The correlations between ASR and OSR were sensitive to systematic changes in the 5 parameters we used to compute these ratios parameter values. In 2009, none of the parameter values resulted in a significant association between ASR and OSR (Table 2). In 2010, the significant positive correlation observed between the baseline values of ASR and OSR persisted for 13 of the 24 parameter values, the rest were positive but nonsignificant (Table 2). In 2011, the positive but nonsignificant relationship between ASR and OSR originally observed with the baseline values, became significantly negative at 8 of the 24 parameter values. When all parameters were altered simultaneously for ASR and OSR, the observed association between them at a 0 day lag was consistent with the baseline association for all 3 years.

Table 2
ASR and OSR cross-correlation coefficients for 0 day lag when parameters for calculating sex ratios were modified for the sensitivity analysis (see Table 1)

ASR \ OSR	Year	Baseline values	Arrival date	Departure date	T_i	T_f	All parameters
Baseline values	2009	-0.03 (0.70)	-0.01 (0.88)	0.04 (0.67)	0.02 (0.81)	-0.007 (0.94)	0.001 (0.98)
	2010	0.22 (0.01)	0.21 (0.02)	0.16 (0.06)	0.22 (0.01)	0.18 (0.04)	0.13 (0.15)
	2011	0.09 (0.36)	0.13 (0.15)	-0.30 (<0.001)	-0.28 (<0.01)	0.10 (0.26)	-0.06 (0.51)
Arrival date	2009	0.04 (0.65)	-0.02 (0.79)	0.10 (0.26)	0.09 (0.35)	0.04 (0.70)	0.01 (0.93)
	2010	0.20 (0.03)	0.20 (0.02)	0.13 (0.14)	0.19 (0.03)	0.16 (0.07)	0.14 (0.11)
	2011	0.02 (0.83)	0.03 (0.73)	-0.52 (<0.001)	-0.52 (<0.001)	0.03 (0.75)	0.02 (0.81)
Departure date	2009	0.04 (0.64)	-0.02 (0.80)	0.10 (0.26)	0.08 (0.34)	0.03 (0.70)	0.01 (0.92)
	2010	0.20 (0.03)	0.20 (0.02)	0.13 (0.14)	0.19 (0.03)	0.16 (0.07)	0.14 (0.11)
	2011	0.02 (0.83)	0.03 (0.73)	0.53 (<0.001)	-0.52 (<0.001)	0.03 (0.75)	0.02 (0.80)
All parameters	2009	0.15 (0.08)	-0.04 (0.69)	0.04 (0.68)	0.04 (0.62)	0.02 (0.93)	-0.03 (0.78)
	2010	0.15 (0.08)	0.14 (0.11)	0.22 (0.01)	0.13 (0.13)	0.12 (0.16)	0.22 (0.01)
	2011	0.02 (0.99)	0.02 (0.83)	-0.52 (<0.001)	-0.53 (<0.001)	0.01 (0.95)	0.03 (0.71)

Correlation coefficient with *P* value in parenthesis is shown for all possible correlations per year, significant correlations are shown in boldface.

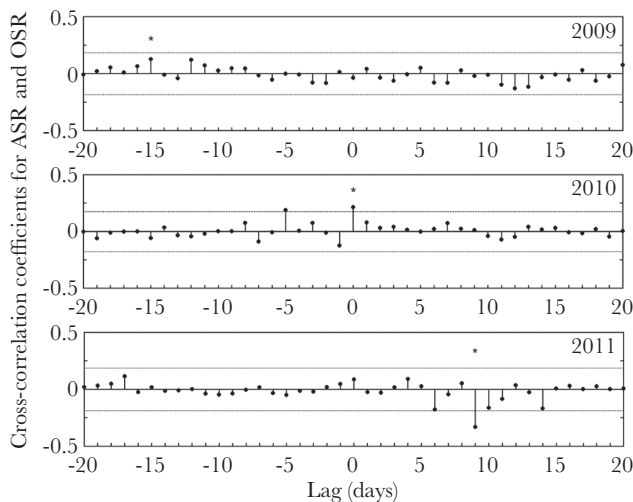


Figure 3
 Correlation coefficients of cross-correlation analysis between time series of ASR and OSR of snowy plovers during 3 years of study. The *x*-axis indicates the number of days by which ASR leads (- lags) or lags (+ lags) OSR. Horizontal dotted lines show approximate upper and lower confidence bounds of cross-correlations assuming ASR and OSR are uncorrelated. The asterisks show peak correlations in each year.

Peak cross-correlations for the different modified parameter values varied in direction and lag each year (results not shown). In 2009, no peak cross-correlations observed were significant. In 2010, peak cross-correlations were significant in 15 of the 24 parameter values (14 positive, 1 negative; lags between -12 and 0). In 2011, all 24 peak cross-correlations were significant (9 positive, 15 negative with lags between 0 and 14).

DISCUSSION

By estimating temporal variation in both ASR and OSR in a wild bird population, our work provided 2 major results. First, ASR and OSR were both male biased, and OSR showed greater temporal variation than ASR. Second, cross-correlation tests failed to detect a consistent relationship between ASR and OSR: in 2 study years (2009 and 2011) ASR and OSR were uncorrelated, whereas in 1 study year (2010) these ratios showed as small positive correlation.

Additionally, the sensitivity analysis showed that slight changes in the parameters used to estimate ASR and OSR had large impacts on their correlation coefficients.

Bias and temporal variation of sex ratios

Male-biased ASR in the snowy plover’s Ceuta population is consistent with male-biased ASR reported in other populations of snowy plovers (Stenzel et al. 2011) and with generally male-biased ASRs reported in birds (Donald 2007; Pipoly et al. 2015). In birds, higher mortality in females than males (Promislow et al. 1992; Liker and Székely 2005) is the likely cause for male-biased ASR (Gerlach and Le Maitre 2001; Githiru and Lens, 2006; Székely et al. 2006; Kosztolányi et al. 2011). Biases can be reinforced by higher dispersal and/or further migration of females (Greenwood and Harvey 1982; Kjellen 1994; Clarke et al. 1997; Dale 2001; Stouffer et al. 2003; Catry et al. 2005; Steifetten and Dale 2006) or by sex differences in time of arrival to the breeding grounds (Clutton-Brock and Parker 1992; Payne et al. 2011). Male-biased ASRs observed in local populations could also be a consequence of higher mobility of one sex during the breeding season (Küpper et al. 2012) coinciding with a higher turnover and shorter periods spent at a given breeding site by females than males. Consistent with this, snowy plover females spent less time in Ceuta than males (mean throughout the 3 years, females: 81.31 ± 4.5 days, $n = 83$ females; males: 93.72 ± 3.32 days, $n = 110$ males, $t_{159} = -2.22$, $P = 0.03$). If females have higher mobility than males, more unringed females than males could visit the breeding site for breeding reducing the true sex ratio bias. However, we did not find differences between the numbers of newly ringed males and females across the study years (males: 15, 35, 22; females: 21, 27, 26; $\chi^2_2 = 2.34$, $P = 0.31$, $n = 3$ years).

Similarly to ASR, median OSR was also male biased in Ceuta. In comparison with ASR, daily estimates of OSR showed higher temporal variation throughout the breeding seasons as shown by larger interquartile ranges of OSR compared with ASR using a conservative test. This is consistent with theoretical models that suggest that OSR is a dynamic outcome of mating and parental decisions (Kokko and Jennions 2008), whereas ASR is largely influenced by demographic processes and therefore should vary less (Székely et al. 2014). Given the strong variation in OSR with shifts from strong male bias to strong female bias initially expected, we had predicted the overall OSR to be slightly male biased or unbiased. However,

we found a strong male bias in OSR. This may be because periods with strong female bias were scarce and brief, implying either that females in the breeding pool remate very quickly or only stay at the site for brief periods of time.

The biases of both ASR and OSR are conservative because both estimates were determined using the previously marked part of the population only. This is a consequence of our field methods because most adults are trapped on the nest and therefore must have bred at least once at the site previously. As polyandrous plover females have higher mating opportunities than males (Székely et al. 1999), it is plausible that a larger proportion of males than females remained unmarked and therefore the sex ratio bias toward males could be even stronger as suggested by demographic models in other polyandrous plover populations (Kosztolányi et al. 2011).

We are aware of only 2 studies in a single species analyzing temporal variation in ASR throughout the breeding season. On these studies, ASR was highly variable throughout the year and markedly different between populations of the Trinidadian guppy (Pettersson et al. 2004; Arendt et al. 2014), as some populations exhibit an overall male-biased or female-biased ASR or no bias at all (Pettersson et al. 2004). Trinidadian guppies present a complex mating system: females are overall promiscuous but males may use either a courting or a sneaking tactic to mate with females (Houde 1997) depending on environmental factors such as light (Chapman et al. 2009), food availability, or parasites (Kolluru et al. 2009). However, given that ASR is a strong predictor of mating system in shorebirds (Liker et al. 2013), it will be interesting to explore whether the variability in ASR will also explain the complex and varying mating system in guppies. By contrast, snowy plover populations are consistently polyandrous and exhibit ASRs that are more stable in time and consistently male biased throughout populations (this study; Warriner et al. 1986; Stenzel et al. 2011; Carmona-Isunza et al. 2015). Consistency of the sex ratio bias might be negatively correlated to the flexibility of the mating behavior. For example, mating systems might show little flexibility in species where ASRs remain stable through time, whereas populations with variable mating systems may exhibit more variable ASRs. Comparative phylogenetic studies are needed to test whether this is a widespread pattern.

Correlation between ASR and OSR

There was no consistent relationship between ASR and OSR. We found a weak correlation in 1 year and no correlation in the other 2 years. Unpublished population estimates of ASR and OSR indicate that the correlation in other bird and mammal populations may be positive (approximately 0.4–0.5, Liker personal communication, using data from Whitfield 1990; Mitani et al. 1996). However, although theory indicates that OSR is more labile than ASR (Kokko and Jennions 2008), a consistent relationship is not necessarily expected.

Diverse mating systems may influence the relation between ASR and OSR. For example, ASR and OSR are expected to be correlated in monogamous populations, where males and females have similar time-in and time-out periods. In contrast, in polygamous populations with sex difference in the extent of care, the time-in and time-out of males and females may differ, and this difference, in turn, lead to weak (or no) relationship between ASR and OSR. For example, birds tend to have male-biased ASRs, and because they exhibit social monogamy and biparental care of the young, the male-biased ASR is expected to translate into male-biased OSR (Donald 2007), yielding a potentially strong correlation between them. It is important to note that in species where extrapair

paternity occurs as a mating strategy such as many passerine birds establishing female time-out and time-in periods is not trivial. Contrastingly, in mammals that tend to exhibit female-biased ASR, the OSR may still be male biased, given that parental care is largely provided by the females (Székely et al. 2014), and this may translate into a potentially poor correlation between ASR and OSR. It will be interesting to undertake multi-population studies evaluating ASR and OSR in populations with different mating systems. Taxa with high variation in mating system like fish, frogs, and other avian species pose good models to indagate differences in how ASR and OSR relate to each other.

We observed a high stochasticity in the relationship between ASR and OSR. This may be the result of environmental fluctuations (e.g. climatic) and/or density-dependent processes (e.g. competition for territories or food) that impact population dynamics, physiology, and breeding activity of individuals. Fluctuations observed in correlations of ASR and OSR throughout the years may be related to the constraints of our data set. The number and proportion of previously marked breeders in our sample decreased in each year (see Methods). The sex ratios of marked and unmarked plovers may have been different, if trapping probability is altered by sex-specific mobility and breeding activity. This may have resulted in a lower accuracy for estimations particularly in 2010 and 2011 in comparison with 2009. In line with this argument, the sensitivity analysis changed the result of the correlation test less dramatically in 2009 than in the other 2 years. Further studies are needed to understand to what extent these fluctuations and density-dependent processes interact to produce variation in observed sex ratios.

Lagged correlation between ASR and OSR

There was no consistent time lag for peak correlations between OSR and ASR. A negative peak correlation coefficient is predicted if the male bias in ASR is positively related to female brood desertion which affects the OSR several days later. This is a plausible explanation as it is expected that if remating opportunities of females increase, females adjust their degree of involvement in parental care (Kokko and Jennions 2008). However, we observed this only vaguely in 1 of the 3 years, whereas the mating and parental care patterns did not differ substantially across the three years (Küpper C and Cruz-López M, unpublished data).

ASR and OSR estimation accuracy

Estimating ASRs in wild populations is challenging as behavioral and ecological differences between males and females can make one sex more conspicuous than the other and can give rise to additional biases in ASR estimates (Donald 2007; Székely et al. 2014). ASR estimates based on capture–mark–recapture methods can deal with sex differences in detectabilities, at least partially (Veran and Beissinger 2009; Pickett et al. 2012), but these procedures are not always feasible because the models involved require detailed estimates of a range of demographic parameters for males and females.

Estimating OSR in wild populations is similarly challenging because the reproductive availability of an organism is rarely known. There is no formal consensus on how OSR should be estimated in wild populations and therefore several methods have been used to estimate it. OSR has been estimated during surveys where the observer establishes whether the individual is paired or provides parental care to decide whether it is available to breed or not (e.g. Whitfield 1990). Other studies follow the methodology of

Clutton-Brock and Parker (1992) and estimate OSR using population estimates of time-out periods of males and females and ASR estimations (e.g. Mitani et al. 1996). However, the latter approach allows only to know a single OSR estimate per breeding season and therefore is not suitable to capture the temporal variation that exists. We argue that although OSR may be a useful indicator of breeding opportunities, it cannot replace ASR for 3 reasons: 1) it is not trivial to judge whether an individual is sexually active or not, 2) we demonstrated that it is less stable in time than ASR, and 3) we also showed that OSR biases do not necessarily reflect ASR biases, at least in a polygamous population.

In this study, we combined survey data with highly resolved information about the apparent breeding status of individuals to estimate ASR and OSR at the same time. This approach addressed differences in male and female detectability and allowed us to study intensively ASR and OSR variation over time periods. Importantly, our sensitivity analysis showed that a small change in the estimates for arrival, departure, and time-out periods alters the observed relationship between ASR and OSR dramatically. Sensitivity analyses as employed here can help to deal with uncertainties of the breeding status of an individual, especially in polygamous and promiscuous populations where individuals might be paired but still seeking copulations.

In conclusion, we found no consistent relationship between ASR and OSR in a polygamous wild bird population across multiple years. Estimating variation in sex ratios remains challenging, but its estimation is essential to understand the dynamics of mating and parental care systems as comparative studies suggest that breeding behavior and sex ratios are tightly linked (Liker et al. 2013, 2015). We argue that more parallel estimates of ASR and OSR in wild populations are necessary for comparative and multi-population studies that examine the influence of sex ratios on social behavior and their relationship under different mating system contexts.

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