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ORIGINAL ARTICLE

Courtship behavior differs between monogamous and polygamous plovers

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Abstract Courting, accessing, and/or competing for mates are involved in sexual selection by generating differences in mating success. Although courtship behavior should reflect intensity of mating competition and sexual selection, studies that compare courtship behavior across populations/species with different mating systems subject to differing degrees of mating competition are scanty. Here, we compare courtship behavior between two closely related plover species (*Charadrius* spp.): a polygamous population of snowy plovers and a socially monogamous population of Kentish plovers. Consistently with expectations, both males and females spent more time courting in the polygamous plover than in the monogamous one. In addition, courtship behavior of males relative to females increased over the breeding season in the polygamous plover, whereas it did not change in the monogamous one. Our results therefore suggest that courtship behavior is a fine-tuned and informative indicator of sexual selection in nature.

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Introduction

Mating systems are associated with the sexual selection acting on males and females (Andersson 1994; Shuster and Wade 2003; Jennions and Kokko 2010; Kokko et al. 2012; Fritzsche and Arnqvist 2013). Sexual selection is expected to be stronger in polygamous populations since variation in mating success among individuals of the sex that competes more intensively for mates tends to be higher than in monogamous populations. The relationship between sexual selection and mating competition is revealed by theoretical and comparative studies that show sex-role reversal, increased sexual dimorphism in size, weaponry, and/or ornamentation in polygamous taxa (Møller and Pomiankowski 1993; Székely et al. 2000; Pérez-Barbería et al. 2002; Wilson et al. 2003; Fairbairn et al. 2007; Rosenqvist and Berglund 2011). However, not only secondary sexual characters such as ornaments and armaments can influence reproductive success, but also behaviors that help individuals enhance their access to mates, such as courtship displays. Numerous studies have shown that courtship displays are variable across species and populations and have attributed this variation to differences in their morphology or habitat, or to avoid hybridization in sympatric species (van den Assem and Werren 1994; Hankison and Ptacek 2007; Quinn and Hews 2010; Pedroso et al. 2013; Wang et al. 2015), but there is limited information on whether differences in courtship behavior are associated with differences in their mating systems (but see Hollis and Kawecki 2014; Parra et al. 2014).

The strength of mating competition, and therefore sexual selection, may exhibit temporal variation in natural populations (Grant and Grant 2002; Kasumovic et al. 2008; Siepielski et al. 2009). A common predictor of this variation is the operational sex ratio (OSR), i.e., the ratio of sexually active males to females (Emlen and Oring 1977; Kvarnemo

and Ahnesjö 1996), which may fluctuate dynamically throughout the breeding season (Forsgren et al. 2004; Kasumovic et al. 2008). If OSR is biased towards one sex, more intense sexual selection among the overrepresented sex is expected. Courtship behavior is labile, and it can be expected to vary dynamically in response to shifts in mating competition and mating opportunities (Kokko et al. 2012; Parra et al. 2014) associated with fluctuations in OSR or other ecological variables. For example, in a wild population of two-spotted gobies (*Gobiusculus flavescens*), males court actively early in the season when OSR is highly male-biased, while females court more actively than males late in the season, when OSR is female-biased (Forsgren et al. 2004; Myhre et al. 2012). Few studies have examined how OSR variation relates to courtship within a single population, and understanding how courtship behavior responds to temporal variations in sexual selection in populations or species with different mating systems may contribute significantly to understanding the dynamics of sexual selection in nature.

Here, we compare the proportion of time spent courting in two wild populations of closely related species: polygamous snowy plovers (*Charadrius nivosus*) in Ceuta, Sinaloa, Mexico, and monogamous Kentish plovers (*Charadrius alexandrinus*) in Maio, Cape Verde. Behavioral comparisons between these two species are feasible for three reasons: (1) snowy plovers and Kentish plovers were considered a single species until recent reclassification based on molecular evidence (Küpper et al. 2009; Dos Remedios et al. 2015), (2) our group has carried out a long-term monitoring on both sites, and (3) both sites are ecologically similar as they are natural salt marshes in tropical regions with mean annual temperatures between 23 and 25 °C. Importantly, both species share similar life histories, behavior, and ecology as both are non-colonial ground-nesting insectivorous birds, but mating system may vary across different populations (Page et al. 2009). Snowy plover populations are generally polygamous as males and females (usually more than males) may re-mate with different mates each breeding season (Warriner et al. 1986). Some Kentish plover populations are polygamous, for example in France, Spain, and United Arab Emirates (Lessells 1984; Amat et al. 1999; Kosztolányi et al. 2009), while others are monogamous, for example in Saudi Arabia and Cape Verde (in Maio, over 90 % of adults keep their mate between successive breeding events; O. Vincze et al. unpubl. data). Therefore, variation in mating system of plovers might be attributed to factors that vary throughout populations, rather than to differences between species. Despite having contrasting mating systems, both species' populations studied present low extra-pair paternity rates (below 5 %; K. Maher et al. unpubl. data).

We analyzed behavioral observations from snowy plovers and Kentish plovers collected during their peak breeding season. We predicted that (1) males and females from the polygamous snowy plover population would spend a higher proportion of time courting than males and females from the monogamous Kentish plover population and (2) females would court more than males (i.e., courtship bias) in the polygamous snowy plover population, since females present a larger frequent mate change compared to males, whereas no courtship bias was expected in the monogamous Kentish plover population. Since previous studies found variation in courtship behavior and mating in relation to time in the breeding season (Székely et al. 1999; Forsgren et al. 2004), we also investigated whether courtship behavior varied within the breeding season.

Methods

Study species and study sites

We studied snowy plovers between April and May 2014 at Bahía de Ceuta, México (23° 54′ N, 106° 57′ W) where the annual peak breeding activity occurs from April till June. We studied the Kentish plovers between September and November 2013 at Maio, Cape Verde (15° 08′ N, 23° 13′ W) where the annual peak breeding activity occurs from September till December. Approximately 30–100 pairs in Ceuta and 100–200 pairs in Maio breed every year around saline lake areas and saltpans ranging from 120 to 382 ha surrounded by mangrove (Ceuta) or sandy shores (Maio). Individuals from both species stay all year round at the study sites (TS pers. obs.), although Ceuta hosts migratory and resident snowy plovers. In both species, males and females incubate two to three eggs for 22–27 days (Vincze et al. 2013), but parental care differs: in the snowy plover, one parent (usually the female) abandons the brood shortly after hatching and pairs up with a new mate, whereas in the Kentish plovers, both parents rear the young until fledging after approximately 25 days.

Monitoring and marking of breeding adults and chicks have been carried out since 2006 and 2007 in Ceuta and Maio, respectively (see details in Székely et al. 2008). We carried out nest searching using a car and/or mobile hide. We captured nesting parents (using funnel traps) and chicks to ring them with a numbered metal ring, and adults additionally with an individual combination of color rings (see details in Székely et al. 2008). Previous intensive ringing efforts allowed us to individually identify between 70–80 % and 80–90 % of breeding adults in Ceuta and Maio, respectively.

Behavioral observations

In each site, we searched for pairs with signs of active courtship behavior (e.g., copulating, flat running), building scrapes (shallow depressions in the soil where eggs are laid later on), and territory defending (e.g., fighting intruders away) using a

car or mobile hide and binoculars. Male plovers usually defend a territory which then females adopt and defend. Although courting and copulatory behaviors can occasionally be seen in neutral grounds as feeding areas, they mostly take place within the territory (Cramp and Simmons 1985). When we found a pair in its presumed territory (non-feeding areas that individuals defend), we recorded their color ring combinations, location (UTM coordinates), distance from observer, and time. Ten minutes after arrival (to allow for the habituation of the subjects to the observer), we recorded the following behavioral categories for each focal male and female by instantaneous sampling (Martin and Bateson 2009), every 20 s during 30 min (90 records per observation): *courting with mate*, fighting with intruders, pecking at prey items, or preening. Following descriptions of a "Scrape-ceremony" and "Mating-ceremony" by Cramp and Simmons (1985), we classified the following behaviors, all of which are present in both sexes, under the *courting with mate* category: side-throwing, scraping, standing by the scrape, standing opposite a mate, flat running, cloaca showing, and copulations. Both species observed in this study present similar sexual behavior, and we detected no different postures or displays to the ones already described (details in Cramp and Simmons 1985).

We recorded one to four 30-min observations per pair (mean±se, 2.30±0.22 complete observations per pair), and each observation was made 1 to 5 days apart (2.81±0.84 days apart, including two exceptional made 14 and 20 days apart, from re-nesting pairs) in the morning or afternoon. The proportion of time spent courting was consistent between morning and afternoon observations (paired Wilcoxon signed-rank test: Ceuta $W=1$, $P>0.20$, $n=4$ pairs; Maio $W=3$, $P>0.50$, $n=5$ pairs). All observations lasted 30 min, and whenever focal subjects were hidden from our sight, we recorded them as not seen. On average, in 8.7 % of records, individuals were unseen or covered, and therefore, no behavior was recorded. If individuals left the area and were out of sight for more than 5 min, the observation was stopped and deemed incomplete. We verified that scrapes found had no eggs to ensure that pairs had not initiated incubation yet and were observed in a similar reproductive stage as we were unable to know laying dates for all pairs. We observed a total of seven breeding pairs in Ceuta and 13 pairs in Maio. To maximize our sample size and avoid pseudoreplication, we used in the analysis only the first complete observation for pairs that were observed more than once in Ceuta (six pairs) and Maio (eight pairs). Of seven pairs observed in Ceuta, three had both adults color ringed, three had only one adult color ringed, and one pair had neither adult color ringed. In Maio, all pairs observed had both adults color ringed. We identified unringed birds in Ceuta using unique individual characteristics (e.g., plumage marks or limping) and their location, since snowy plovers are highly territorial (Warriner et al. 1986). All behavioral observations were recorded by the same observer (MCC-I).

Statistical analysis

To analyze the difference in the proportion of time spent courting between species, we counted the total number of records under the *courting with mate* category and the total number of effective records (90 records per observation minus records where the focal subject was covered or not seen) across the first observation of each male and female. Using the total number of courtship records and the total number of effective records with no courtship, we analyzed the proportion of time spent courting within each species separately for males and females using generalized linear models (GLMs) with a logit link function and a quasibinomial error structure to account for overdispersion (Crawley 2003). Quasibinomial error structure is appropriate for overdispersion rates of up to 10 (Crawley 2003); in our models, overdispersion rates were 7.7 and 8.4, respectively, in males' and females' models. However, we further tested the robustness of our results comparing courtship ratios of both species using a non-parametric Mood's median test which accounts for unequal variances (Kasuya 2001).

To investigate differences in the proportion of time spent courting by males and females (courtship bias) between species, we used a linear model (LM) using the z score of the difference between proportions of time spent courting by males and females as response variable. The main factor included in all models was species with two categories: snowy plover (polygamous) or Kentish plover (monogamous). We also included the date of observation (standardized) in our model to control and test for potential within-season variation in courtship, and the two-way interaction between the species and date of observation. Because of the small sample ($n=20$ pairs), we restricted the models to two explanatory variables and one interaction to avoid overparameterization (Crawley 2003). From saturated models that included all explanatory variables and the two-way interaction of interest, non-significant interaction and terms were successively backwards eliminated starting with the largest P value until minimal adequate models were reached (Crawley 2003). We report the significance of the increase in deviance resulting from model simplification (using F tests for GLMs and chi-square tests for LMs) as well as the coefficients for all variables kept in every final model. The variance inflation factor (VIF; excluding interaction terms) was <5 in all saturated models; hence, our results might not be biased by multi-collinearity. We checked each model for highly influential cases using residuals versus leverage plots and fitted models without points with leverage >0.4 (Crawley 2003). Models including and excluding points with leverage >0.4 yielded consistent results. We assessed the goodness of fit of saturated models using residual plots (Crawley 2003). All analyses and figures were carried out using the "base" package in R (R Development Core Team 2014, Version 3.1.0).

Results

Courtship behavior of males and females

Males and females in the polygamous snowy plover spent a significantly greater proportion of time courting than males and females in the monogamous Kentish plover (GLM: male difference between species 25 %, 17–26 % [mean, 95 % CI], $P<0.01$, $n=20$ males, Table 1a, Fig. 1; GLM: female difference between species 14 %, 8–18 %, $P<0.001$, $n=20$ females, Table 1b, Fig. 1). The difference between species in males and in females remained significant when using a non-parametric test (median test: males: $\chi^2_1=10.76$, $P<0.01$, $n=20$; females: $\chi^2_1=6.28$, $P=0.02$, $n=20$).

Within-season variation

The significant interaction between date of observation and species indicated that courtship behavior had different temporal changes between species (LM: difference between slopes of species, −0.97, −1.75 to −0.19, $P=0.03$, $n=20$ pairs, Table 1c, Fig. 2). In the polygamous snowy plover, females courted more than males early in the breeding season, whereas later on, males courted more than females (LM, 0.91, 0.27–1.55 [β, 95 % CI], $P=0.01$, $n=20$ pairs, Table 1c, Fig. 2). However, in the monogamous Kentish plover, sex bias in courtship behavior was not related to the date of observation (Fig. 2).

Table 1 Courtship behavior in two plover species: polygamous snowy plovers and monogamous Kentish plovers. Proportion of time spent courting in: (a) males and (b) females (generalized linear models, GLM) and (c) sex bias in courtship behavior (linear model, LM)

Models	Model simplification			
	ΔDev	df	F	P
(a) Male courtship (% time)				
Species	211.76	1,19	23.45	*<0.001*
Date of observation	6.26	1,18	0.67	0.42
Date of observation × species	9.80	1,17	1.06	0.32
(b) Female courtship (% time)				
Species	153.12	1,19	18.01	*<0.001*
Date of observation	4.57	1,18	0.51	0.49
Date of observation × species	0.05	1,17	0.01	0.94
(c) Sex bias in courtship behavior				
Species	3.72	1,19	–	*0.04*
Date of observation	1.25	1,18	–	0.22
Date of observation × species	3.78	1,17	–	*0.01*

Variables retained in the final models are shown in italics ($n=20$ pairs). Statistics presented are from model comparisons using F tests (GLM) or χ^2 tests (LM)
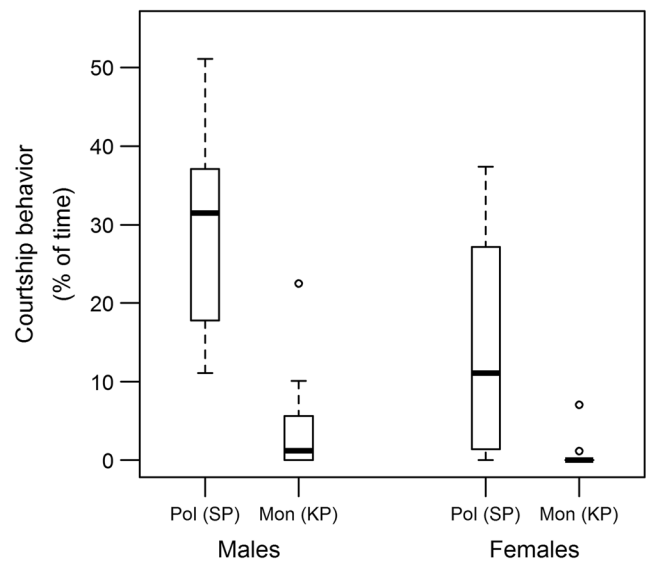
Fig. 1 Courtship behavior (proportion of time spent courting) by males and females in the polygamous (Pol) snowy plover population (SP, 7 males and 7 females) and in the monogamous (Mon) Kentish plover population (KP, 13 males, 13 females). *Boxplot* shows medians (*bold lines*) and 25 and 75 % quartiles (*boxes*). *Whiskers* show extreme data points within 1.5 times the interquartile range. *Open circles* show outliers lying 1.5 times outside the interquartile range

Discussion

Courtship behavior of males and females

We found that both males and females spent more time courting in the polygamous snowy plover than in the monogamous Kentish plover. This result supports the prediction that
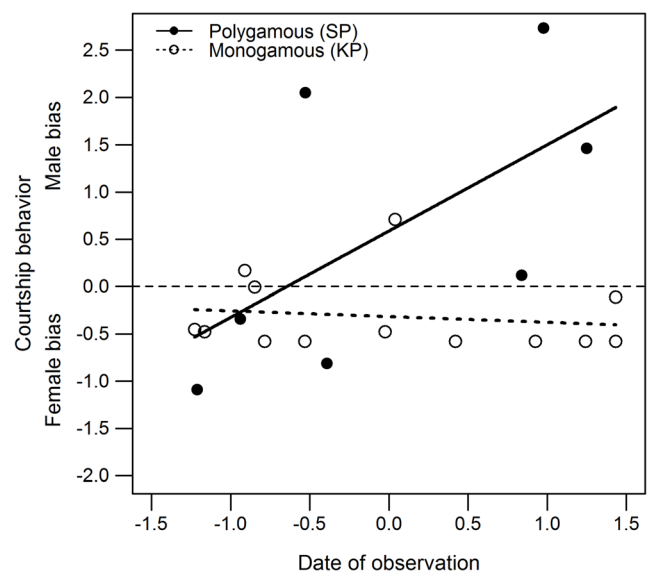

Fig. 2 Sex bias in courtship behavior (*z* score of the difference between males' and females' proportion of time courting) in relation to the date of observation in polygamous snowy plover population (*SP, filled circles and continuous line*) and in the monogamous Kentish plover population (*KP, open circles and broken line*), $n=20$ pairs

levels of mating competition and sexual selection are higher in polygamous species (Shuster and Wade 2003) as these show a higher degree of sexual dimorphism (e.g., Lindenfors and Tullberg 1998; Baker and Wilkinson 2001; Dunn et al. 2001; Ord et al. 2001; Thorén et al. 2006; Price and Whalen 2009) or more ornaments (Møller and Pomiankowski 1993) than monogamous species. This study adds the behavioral perspective to the evidence that mating competition and sexual selection is higher in polygamous than monogamous species.

The difference in the proportion of time spent courting between species could emerge in three ways. First, in a polygamous population, males and females may spend a long time competing to access mates and mate more than once; in this scenario, males and females would have high courting rates to outperform others and breed. In monogamous populations, males and females might be subject to strong mating competition upon their first reproductive event or after a divorce but not in successive events as re-mating with the same partner can reduce the costs associated to mate sampling and bond formation (Adkins-Regan and Tomaszycki 2007; Sánchez-Macouzet et al. 2014). In Maio, over 90 % of mates keep the same mate every year (O. Vincze et al. unpubl. data), so mates familiar with each other might not need to court as frequently as newly formed pairs.

Second, if courtship rate is an indicator of individual quality as suggested by many studies (e.g., Kotiaho 2002; Pariser et al. 2010), then individuals will increase their fitness by preferring mates with high courtship rates. In the polygamous population, as individuals will breed more than once, mate sampling will allow them to compare between potential breeders, and therefore, mates with high courtship rates should have increased probabilities of being preferred. In the monogamous population, mate sampling might happen upon the first reproduction or after a divorce, but as generally individuals keep the same mate in subsequent reproductions, frequency of mate sampling can be low and therefore they will rarely compare between mates with high/low courtship ratios. As emitting courtship displays might be energetically costly (Clark 2012), in a monogamous scenario where mates stay together, high courtship rates are unnecessary and minimum court rates could have a pair bonding and continuing mate evaluation purposes (Wachtmeister 2001).

Third, courtship behavior may differ between snowy plovers and Kentish plovers as a result of their intrinsic genetic differences. Although these species are genetically related, exhibit similar life histories, and were studied in comparable tropical localities, we cannot discard this potential explanation. A more robust comparison would involve several populations of the same species from ecologically equivalent sites but with different mating systems, which are often hard to find. The Saudi Arabian and United Arab Emirates Kentish plover populations pose an interesting alternative as they have contrasting mating systems and are both in desert regions (Kosztolányi et al. 2009; AlRashidi et al. 2011). Nonetheless, we deem unlikely that differences in courtship are explained just by the genetic differences between species. Indeed, genetic differences themselves might not give rise to differences in courtship behavior at least in fruit flies: males of polygamous and experimentally selected monogamous lines held under controlled conditions show similar courtship rates (Hollis and Kawecki 2014). Differences in courtship are more likely given by social or environmental factors rather than only genetic differences.

A social factor that has proved to be related to the strong link between mating systems and competition for mates (Shuster 2009; Parra et al. 2014) is the proportion of males in the adult population (adult sex ratio, ASR; Liker et al. 2013, 2014). While polyandry is related to more male-biased sex ratios, monogamy is related to unbiased sex ratios. Mating competition may increase if the number of one sex increases and the access to mates of the opposite sex is restricted. In line with this, a male-biased sex ratio in the polygamous snowy plover population in Ceuta (unpubl. data) may create high mating competition that leads to the high courtship rates observed. Contrastingly, if numbers of males and females in the population are similar, no strong mating competition is expected. Numbers of males and females in the monogamous Maio Kentish plover are largely the same showing a 1:1 ratio according to field surveys (ratio of males to females: 0.89 ± 0.06, 95 % CI (0.76 to 1.03), t test: $t_{10}=-1.67$, $P=0.12$, $n=11$ surveys, MCC-I and TS unpubl. data), and therefore, no strong competition is expected leading to low courtship rates observed.

In contrast to theoretical predictions, a meta-analysis of experimentally manipulated mating competition (estimated as the operational sex ratio, OSR) found no relationship between courtship behavior and a change in OSR (Weir et al. 2011). The latter meta-analysis study used a number of fish and insect species with contrasting mating and care systems including a number of monogamous and polygamous species. However, if mating system might have an effect in how species respond to shifts in OSR, this was left unmentioned throughout the paper and the type of mating system shown by each species was not controlled for in the analysis. It is currently not known whether monogamous species are responsive to changes in OSR at all or to what extent their courtship rates vary to those of polygamous ones. As our study suggests, the mating system may be a key trait that must be considered in meta-analysis of the kind.

In our study, we could not control for further potential sources of variation in courtship behavior like laying date, male or female ornament variation, individual breeding history, or age. However, in both sites, we observed all the pairs encountered in non-feeding territories defended against intruders and being scraped, suggesting that pairs were

establishing a nesting territory so presumably, the mate choice process had already occurred. We ensured that all pairs were in a similar reproductive stage by limiting our observations only to those where no eggs had been laid. Intriguingly, the number of pairs observed copulating and frequency of copulation during our study were very low in both species. Only in 42 % of snowy plover pairs and in 23 % of Kentish plover pairs were one to two copulations recorded in this study (data not shown). High frequencies of copulation in birds have been related to risk of extra-pair paternity (Birkhead et al. 1987), so low frequencies of copulation observed in this study are consistent with the low rates of extra-pair paternity found in both species.

Within-season variation in courtship behavior

Sex bias in courtship behavior varied within the season in the polygamous snowy plover but not in the monogamous Kentish plover. In the polygamous population of snowy plovers in Ceuta, male courtship behavior (relative to female) intensified as the season progressed. We propose four non-mutually exclusive explanations for this result. First, early-breeding snowy plover males may be in better condition than males breeding later on as is often the case in other bird populations (e.g., Dobson et al. 2008; O'Brien and Dawson 2013). Being of better quality or condition and potentially more attractive than later breeders, early-breeding males might not need to court as much as poor-quality late-breeding males. For example, attractive male guppies courted less often than unattractive males, and this intensity was further modulated by environmental conditions such as ambient light (Reynolds 1993).

Second, the change in snowy plovers' courtship behavior might be responding to changes in OSR. Californian polygamous snowy plover populations have a male-biased adult sex ratio (Stenzel et al. 2011), and similarly, those in Ceuta present a male-biased sex ratio (unpubl. data); even though male snowy plovers provide more extensive care than females in the polygamous Ceuta population, OSR is still expected to become more male-biased because females will rapidly engage in breeding. An increasingly male-biased sex ratio with time of the season should lead to more intense mating competition and courtship behaviors in males, whereas for females, mating competition should decrease. This matches the changes of courtship intensity we observed in the snowy plover in Ceuta (this study). On the other hand, in Maio, males and females have comparable involvement in parental care and the OSR in this population might not be biased. Therefore, mating competition might be constant throughout the breeding season in this population and consequently no temporal change in the proportion of time spent courting rates was observed.

Third, a male bias in the snowy plover population means that late-breeding males may have been mating for the first time whereas late-breeding females were breeding for the second or third time (as female re-mating after brood desertion is common in this population). This male bias in addition to the potential decline in breeding success for late breeders documented in many bird species (reviewed in Verhulst and Nilsson 2008) could result in early-breeding females accelerating their mate choosing and courting phase compared to late ones. This could benefit females by maximizing both chick survival and their time remaining for re-mating, resulting in early-breeding males needing to court less than late ones.

The last alternative explanation to the seasonal pattern of courtship in snowy plovers from Ceuta is that of terminal investment. According to life history theory, if the probability of future reproductions declines, then an increase in current reproduction is expected (Clutton-Brock 1984). Late-breeding snowy plovers might be in lower condition than early breeders, and if their low condition reduces their probabilities of surviving until next year, they might be willing to invest more in that breeding attempt. However, under this explanation, it is unclear why this pattern was not observed in Maio's Kentish plovers, as the same prediction should hold under a monogamous mating system if probabilities of surviving from one season to the next one are similar in monogamous and polygamous populations. Experimental studies in species or populations with different mating systems will help disentangle the underlying causes of the temporal variation in courtship.

In conclusion, we found that closely related species of plovers with contrasting mating systems differed in their time spent courting: the polygamous species spent more time courting than the monogamous one. However, the relationship between courtship behavior and mating system was more complex than initially thought given a within-season variation was found only in the polygamous species. Altogether, our results suggest that courtship behavior may offer a simple and flexible tool to gauge the mating demand of males in relation to females. Despite moderate sample sizes, the species differences reported here were statistically significant, suggesting large effect sizes. For testing the generality of our observations, comparing courtship behavior across different mating systems in other populations or closely related species appears to be a fruitful avenue which may not require large sample sizes. More studies are needed to understand how sexual selection (and different estimates of its intensity) influences mating system evolution. We encourage future studies that combine behavioral estimates of sexual selection (e.g., aggression and courtship behavior) and compare these to other indices of sexual selection across species and populations with diverse mating systems.

Compliance with ethical standards In this study, we investigated two geographically widespread and non-endangered bird species in their natural habitats. The data collected for this study were based only on observations that did not require any capture or manipulation; data collection consisted in observations of pairs at a distance of 10 to 20 m using a hide or a car, carefully avoiding the disturbance of the normal activities of birds. When using a car, we drove only on marked tracks where cars usually drive in order to avoid additional disturbance of the natural habitat. As part of the annual monitoring, birds were caught using funnel traps during late incubation or after hatching of the clutch. Traps were left on the nest/clutch up to 25 min and were shaded to avoid egg exposure to heat; trapping was avoided at extreme heat. Birds were ringed and manipulated by well-trained people. All aspects of the fieldwork were authorized by the national authorities in Cape Verde (Direcção Geral do Ambiente, DGA) and Mexico (Secretaría de Medio Ambiente y Recursos Naturales, SEMARNAT).

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