



Birds choose long-term partners years before breeding



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Pair bonds can provide social benefits to long-term monogamous species alongside their benefits for reproduction. However, little is known about when these bonds form, in particular how long they are present before breeding. Previous studies of pair formation in long-term monogamous birds have been rather data-limited, but for many migratory birds they report pair formation on the wintering grounds. We provide the first systematic investigation of prebreeding association patterns of long-term monogamous pairs by examining entire life histories based on tracking data of migratory whooping cranes, *Grus americana*. We found that a substantial portion (62%) of breeding pairs started associating at least 12 months before first breeding, with 16 of 58 breeding pairs beginning to associate over 2 years before first breeding. For most pairs, these associations with future breeding partners also became unique and distinguishable from association patterns with nonpartner individuals 12 months before first breeding. In addition, 60% of pair associations began before at least one partner had reached nominal sexual maturity. Most pairs began associating in the late spring upon arrival at the summer grounds, while associations beginning at other times of the year were rare. Patterns in the associations of pairs prior to breeding can point to the potential benefits of prebreeding relationships, for instance providing support in competitive interactions or increasing partner familiarity.

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Monogamy is common in nature (Wittenberger & Tilson, 1980) and is the predominant mating system in birds (Black & Hulme, 1996). In many bird species, pairs even show long-term or life-time fidelity, remaining together for multiple breeding seasons (Fowler, 1995). However, unlike in species where mates are chosen every year (Andersson & Simmons, 2006; Ens, Choudhury, & Black, 1996; Taff, Patricelli, & Freeman-Gallant, 2014), pair formation of long-term monogamous animals has not been well studied (but see Black, Choudhury, & Owen, 1996; Ihle, Kempnaers, & Forstmeier, 2015). Understanding this initial pair formation is important not only because pair associations affect social relationships and breeding for years to come, but because the duration of monogamous pair bonds and the timing of their formation can point to the

benefits of long-term monogamy more generally (Owen, Black, & Liber, 1988).

The drivers of long-term monogamy fall into two main, nonexclusive categories: costs of divorce and benefits of partnerships. First, long-term monogamy may be advantageous if the costs of mate loss are high, leading to a gap in breeding, low breeding success or reduced survival in a year following divorce (Ens et al., 1996; Nicolai, Sedinger, Ward, & Boyd, 2012). Some of these high divorce costs could stem from difficulty finding a new partner, as in cases where a population's male-skewed sex ratio produces a shortage of available females and results in mate-guarding behaviour by males (Mathews, 2002; Rodway, 2007; Wittenberger & Tilson, 1980). In addition, in species where courtship is energy intensive, finding a new partner may consume time and energy that could otherwise be devoted to mating or resource acquisition (Nakamura & Atsumi, 2000). Empirical evidence suggests that finding a new mate is also stressful (Angelier, Moe, Clement-Chastel, & Chastel, 2007), pointing to a possible physiological cost of divorce that could drive partners to stay together for multiple years.

Long-term monogamous partnerships could also be favoured if they provide social or fitness benefits that accrue over time, thus

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favouring long-term monogamy over short-term partnerships. Social status in avian species usually increases with age (Verhulst, Geerdink, Salomons, & Boonekamp, 2014) but also with paired status (Black, 2001; Nakamura & Atsumi, 2000), which means that associating with a partner could increase the social status of the individuals in a pair, thereby improving their body condition and fitness (Emery, Seed, Von Bayern, & Clayton, 2007; Poisbleau et al., 2006; Weiß, Kotrschal, & Foerster, 2011). This effect is particularly important for long-term partnerships, where the status of a pair can increase across years (Stehn, 1992). In addition, breeding success increases with pair bond duration in a number of monogamous species (Fowler, 1995; Sánchez-Macouzet, Rodríguez, & Drummond, 2014), especially when one individual already has breeding experience (Leach & Sedinger, 2016); this benefit of long-term pair bonds is consistent with increased behavioural or hormonal compatibility of pairs over time (Laubu, Dechaume-Moncharmont, Motreuil, & Schweitzer, 2016; Ouyang, van Oers, Quetting, & Hau, 2014). Forming a monogamous partnership prior to first breeding may thus increase breeding success, particularly during a pair's first breeding attempt.

Existing literature about the benefits of long-term monogamy has focused on the benefits of remaining in an established pair bond (i.e. the costs of divorce; Black, 1996; Culina, Radersma, & Sheldon, 2015; Ens et al., 1996), but these studies have rarely addressed the behaviour of pair members prior to mating. To date, most studies that provide evidence for the benefits of monogamy have defined a pair bond as beginning at the time of first breeding (e.g. Lewis, Elston, Daunt, Cheney, & Thompson, 2009; Sánchez-Macouzet et al., 2014), which ignores the possibility that monogamous breeding pairs could begin associating long before breeding takes place. At the same time, for some species it has long been observed that monogamous pairs arrive on their breeding grounds already paired (e.g. in waterfowl, storks and others: Lack, 1940; Robertson & Cooke, 1999; but see Pickering, 1989), and the limited number of studies of pair formation suggest that pairs can form long before first breeding (Choudhury & Black, 1994; Fisher, 1975; Owen et al., 1988; Stehn, 1997). However, these few studies of initial pair formation have been limited in their scope, focusing almost exclusively on observations during the wintering period (Evans, 1979; Ganter, Boyd, Baranyuk, & Cooke, 2005; Johns, Goossen, Kuyt, & Craig-Moore, 2005; Owen et al., 1988; Weller, 1965; but see Minton, 1968) and were thus unable to determine the actual time at which pair members began associating.

To identify whether high divorce costs and/or the benefits of long-term partnerships could be important drivers of long-term monogamy, we investigated prebreeding association patterns of pairs of whooping cranes, *Grus americana*, a long-term monogamous bird species. The time at which prebreeding associations begin can indicate the types of benefits provided by monogamous partnerships; if pairs begin to associate over a year before they first breed, then these associations likely provide a fitness benefit directly to one or both partners. In the extreme, if pair members gain status and social support from being associated with their future partner, then pairs could begin associating even before one or both partners reach sexual maturity. Conversely, if monogamy is driven solely by high divorce costs and partnerships provide no direct benefits, we would expect pairs to form shortly before first breeding (e.g. in the winter preceding first breeding or upon arrival on the breeding grounds). In addition, because one possible driver of high divorce costs is an unbalanced sex ratio that makes rearing difficult (Culina et al., 2015), we also examined the number and sex ratio of unpaired and nonbreeding adults as possible drivers of long-term monogamy. We used a high-resolution monitoring data set of a population of whooping cranes, which enabled us to identify the association patterns of breeding pairs at a

temporal resolution that has not previously been possible using only behavioural observations or ringing data.

METHODS

Data Sets

We used data from the location and nesting databases of the reintroduced eastern migratory population of whooping cranes (Whooping Crane Eastern Partnership (WCEP), 2016). This population is composed mostly of released captive-reared birds, and any wild-hatched chicks are captured, so every individual in the population is identified with a unique leg band and a very high frequency (VHF) transmitter and ages and sexes are known for the entire population. The location database consists of locations of individual birds in the population over their lifetimes based on VHF telemetry and visual observations; although most birds do not carry global positioning system (GPS) transmitters, the detection probability of an individual in a 3-month period is >99% (Servanty, Converse, & Bailey, 2014). Additional details of reintroduction techniques and monitoring are available in Urbanek, Fondow, Zimorski, Wellington, and Nipper (2010) and Servanty et al. (2014). The WCEP also keeps records on birth and death dates of individuals, which we used to determine individual ages and validate mortality dates obtained from last observations in the location database. The sex of all individuals is determined genetically. We used all available monitoring data from the beginning of the reintroduction effort (2001) through November 2015.

The nesting database consists of observations of all nests during the breeding season, including their initiation dates and hatching or failure dates. Nests were detected and monitored daily using the same methods as for the location database (i.e. locating individuals via telemetry and then observing nest presence), and some nests were additionally monitored with video cameras placed near the nest. These observations on the ground were supplemented by regular flights over the breeding area, which were particularly important because of the small number of nests that were blocked from ground observation (e.g. by vegetation). It is highly unlikely that nests were present but not detected because of the intensity of monitoring before and during the breeding season (Converse, Royle, Adler, Urbanek, & Barzen, 2013); the relatively small population size and limited spatial area of the breeding grounds also made it possible to observe every nest. Nests were monitored daily during the breeding season in all years and only on rare occasions was there a gap of 1–2 days in monitoring. For full details of the monitoring protocol see Urbanek, Zimorski, Fasoli, and Szyzkowski (2010) and Converse et al. (2013). We used data on all nests from the first nesting attempt in the population, in 2005, through 2015.

Amount of Time Spent with Breeding Partner

We used the location database (1) to identify whether associations between breeding pairs were distinguishable from nonbreeding duos and, if so, (2) to detect the timescale at which this unique association began. First, for each breeding bird, we calculated the proportion of time spent with each other bird (of both sexes) in the population at 90-day intervals before and after first breeding. For each observation of a focal bird during a given time period, we identified all birds observed at the same location as the focal individual (including both its future partner and non-partners). Because points in the location database were obtained by visual confirmation of VHF locations, birds seen by the same observer at the same time are assigned identical coordinates in the database, making assignment of a minimum buffer distance unnecessary. Based on these co-occurrences, we then calculated the

proportion of observations where each other bird was present, in other words the proportion of time the focal individual had spent with each other bird during that time period. We performed this calculation at 90-day intervals during the prebreeding period (i.e. within 90 days prior to first breeding, within 91–180 days prior to first breeding, etc.) and the postbreeding period (i.e. within 90 days after breeding, within 91–180 days after breeding, etc.) up to 4 years before first breeding and 1 year after first breeding, as long as both partners were alive. We also repeated these same analyses considering only birds of the other sex; this alternative analysis yielded qualitatively similar results, so we present results including birds of both sexes below.

We used these data to determine the timescale at which birds began spending more time with their future partner than with any other bird. For each focal bird and at each timescale, we calculated the proportion of time the focal bird spent with each other bird relative to the amount of time spent with its breeding partner by subtracting the proportion of time spent with each other bird from the proportion of time spent with its breeding partner during that time period. A positive value indicates that the focal individual was associating more with its breeding partner than with the other bird, while a negative value indicates that the focal individual associated more frequently with the bird that did not become its partner than with its partner during that time period. To analyse these data, we then found the minimum value of all nonpartner bird-to-focal-bird calculations, which identified the most preferred nonpartner in each time period (i.e. the nonpartner with which the focal individual spent the greatest proportion of its time). Then, for each 90-day period before and after first nesting, we found the 10% and 90% quantiles of this minimum value across all birds and used the lower value to identify the time interval during which most birds (90%) began associating preferentially with their partner.

Beginning of Pair Association

While the above metric examined when associations of breeding pairs became unique relative to other (nonpair) associations, we also employed a 3-month association criterion established by a previous study (Servanty et al., 2014) to identify the beginning of association of future breeding pairs, independent of any other associations the pair members may have. We considered a breeding pair to have begun associating if they were observed together at least once per month for three consecutive months, based on a previous analysis showing that 3 months of association is the threshold between short-term associations and mid- or long-term pairs (Servanty et al., 2014; Supplementary Fig. S1). Since pairs of whooping cranes associate year-round but can separate for short periods to forage, we required birds to be seen together at least once per month but did not require birds to be located together at every observation within a month (Swengel, Archibald, Ellis, & Smith, 1996). Our criterion also allows for the possibility that a pair could be co-located with other birds simultaneously (e.g. due to shared feeding areas of prebreeding and wintering birds, or due to association with offspring), since it does not require that pair members associate exclusively with one another. The majority of individuals were observed multiple times each month, meaning that this metric of association is usually based on multiple observations of a pair during a month. For one pair, we did not observe pair members together for at least three consecutive months prior to breeding; in this case, we considered the beginning of association to be the month in which the nest of that pair was first detected.

Using the same framework as above, we also analysed association patterns for duos of birds that did not become breeding pairs ('null pairs'). This null data set allowed us to identify patterns

present in the associations of breeding pairs that were not present in nonpair associations. For each individual in the population, we identified any potential partners, which were all birds of the opposite sex that were 'available' to breed. In order to be considered 'available', a potential partner was required to be of breeding age during at least one summer when the focal bird was of breeding age and, if the potential partner had bred previously, its previous partner could not still be alive. This definition allows for re-pairing following the death of a partner but not for possible divorces; divorce can occur in whooping cranes but is rare and therefore unlikely to substantially affect our estimates. For each of these null pairs, we identified the month of first association as we did for actual breeding pairs (i.e. as the beginning of the period when birds were first observed together for three consecutive months). We analysed the month of first association of both breeding pairs and null pairs with kernel density estimation and visual inspection; kernel density estimation was performed using the 'density' function in R (R Development Core Team, 2016), including using the recommended bandwidth (based on methods from Scott, 1992).

Prebreeding Association Duration

For each breeding pair, we calculated the prebreeding association duration, the number of months elapsed between a pair's first association (i.e. the beginning of the pair's first three consecutive months observed together) and that pair's first breeding attempt (as identified in the nesting database) (e.g. Fig. S1). We also noted the ages of each member of a pair at the time of first association, which we used to investigate the relationship between the duration of prebreeding association and the age of the birds in a pair. Since successful nesting cannot occur until both partners have reached sexual maturity (3 years old in this species; Archibald & Lewis, 1996; Travsky & Beauvais, 2004; Urbanek & Lewis, 2015), we examined the age of the younger partner in a pair, which allowed us to test whether pairs begin associating before they could plausibly begin breeding. To analyse this relationship, we built a generalized linear model that modelled prebreeding association duration (in months) as a function of the age of the younger bird in the pair at the time of first association (in years). We used a Gaussian distribution with a log link, since prebreeding association period was bounded at zero.

Sex Ratio and Nonbreeding Birds

To examine the possibility that monogamy is driven by high divorce costs, we identified all unpaired and nonbreeding birds of each sex in the population. In each year, nonbreeders were defined as birds of reproductive age (i.e. at least 3 years old) that were observed during the summer and were not observed nesting. These birds may or may not have been paired. In addition, we identified the subset of these nonbreeders that were unpaired, which were birds that had never formed a 3-month association or that had previously nested but whose partner had died. Including this subset takes into account any years when birds were paired (and therefore not available for a new partner) but did not nest. We examined the number and sex ratio of these non-nesting and unpaired birds over time.

RESULTS

Our data set consisted of 197 breeding attempts of 89 individuals forming 58 pairs. There were seven divorces, four of which involved re-pairing by both partners and three of which involved re-pairing by the female only. In addition, there were 13

cases of re-pairing following the death of one partner during the study period (through summer 2015).

Association patterns of birds that became breeding pairs were distinguishable from association patterns with nonpartners at long timescales. When we examined the amount of time each breeding bird spent with its most preferred nonpartner relative to its future partner, we saw that 90% of birds started spending time preferentially with their future partner between 270 and 360 days (9–12 months) before first nesting (Fig. 1). Results were qualitatively similar when we considered all other birds, rather than only the most preferred nonpartner, with a similar increase in association with the future partner over time and the mean preference value for the future partner increasing above zero approximately 1 year before first nesting. The degree to which most birds preferred their partner in the year directly preceding nesting was comparable to that during nesting and in the year after nesting (Fig. 1). On average, birds were observed with their partner for 77% of the time during the year preceding first nesting ($SD = 0.22$) and were observed with their partner 72% of the time during the year following first nest initiation ($SD = 0.18$) (Fig. S2). In comparison, the average bird spent 21% of its time with its most preferred nonpartner during the year preceding nesting ($SD = 0.11$).

We defined the beginning of a pair's association as the beginning of the first period when its members were observed together for three consecutive months (Fig. S1). These pair associations began between 0 and 56 months (4.5 years) before first breeding. The largest number of pair associations began 11–12 months before first breeding, with peaks at 24 months and 36 months prior to the eventual date of first breeding (Fig. 2). Sixty-two per cent ($SE = 56$ –68%) of pairs began associating at least 1 year before first breeding. The mean prebreeding association duration was 15 months (median = 12 months), which is on the order of the time of preferential association from the previous analysis (9–12 months).

Most breeding pairs began associating in spring, where 60% ($SE = 54$ –66%) of pair associations began in March, April and May (Fig. 3). This pattern was not present in null pairs, which were male/female duos that could have become breeding pairs based on their ages and simultaneous unpaired status but did not. Among null pairs, only 13% ($SE: 12$ –14%) of these duos associated for 3 months or more, compared with 98% of breeding pairs. Within the 13% of

null pairs that did associate for three consecutive months, there was no single identifiable time of year at which their associations began (Fig. 3).

The duration of the prebreeding association period was related to the age of the younger member of a pair, where pairs with younger members associated for a longer time before breeding ($\beta = -0.54$, $SE = -0.63$, -0.45 ; Fig. 4). This negative relationship was driven largely by the long prebreeding association period for pairs that formed before one partner had reached sexual maturity (nominally age 3: Archibald & Lewis, 1996; Travsky & Beauvais, 2004; Urbanek & Lewis, 2015); even so, of the pairs that began associating after both partners had reached sexual maturity, over half (52%, $SE = 42$ –63%) still associated for over 6 months before nesting.

The sex ratio in the population was slightly skewed towards males at all points in time (Table S1), and there were a substantial number of unpaired and nonbreeding individuals of both sexes present in the population at any time (Fig. 5). Most birds spent only 1 year unpaired or not breeding after reaching sexual maturity, and the majority of unpaired and nonbreeding birds were young (3 and 4 years old; Fig. S3).

DISCUSSION

We found that monogamous whooping cranes began associating with their future partners long before breeding, and that many associations began even before one or both partners reached sexual maturity. Previous studies of long-term monogamous birds have assumed that pair bonds form shortly before first breeding (Lewis et al., 2009; Sánchez-Macouzet et al., 2014) or in the winter preceding first breeding (Stehn, 1997). In contrast, our results indicate that monogamous pairs could form years before breeding begins, if the associations we detected are indicative of early pair-bonding behaviour. The presence of early-life associations suggests that pairs may derive direct benefits from associating with their breeding partner, and that long-term monogamy in this species is unlikely to be driven solely by a high cost of divorce.

The high frequency of associations that began before at least one individual in a pair had reached sexual maturity is particularly suggestive of direct benefits of early-life associations. The age of

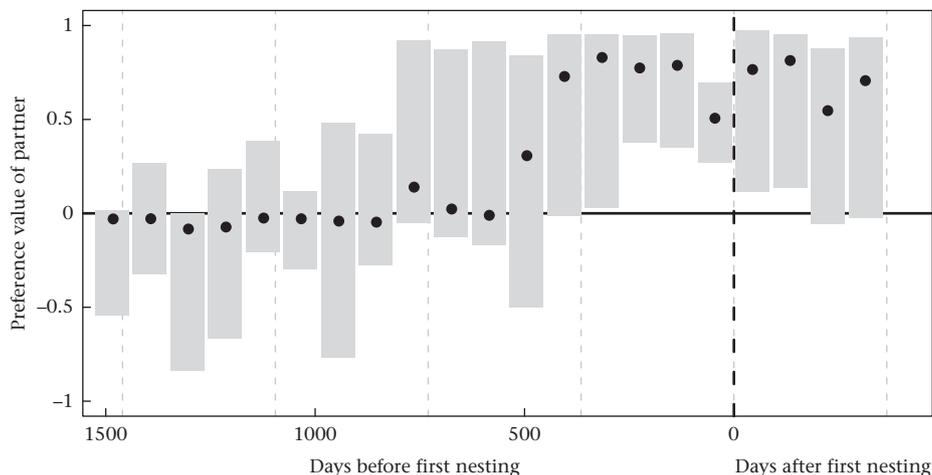


Figure 1. Amount of time spent with partners relative to nonpartners. The preference value is the difference in the proportion of time that a focal individual was observed with its partner and the proportion of time that it was observed with its most common nonpartner associate in each 90-day interval. Positive values (above the solid line) indicate that a bird was spending time primarily with its future partner. Grey boxes show values between the 10% and 90% quantiles and black points show the mean for each 90-day time interval. Light grey dashed lines show 1-year intervals and the dashed black line represents the date of first nesting. Approximately 1 year before first breeding, the amount of time spent with a future breeding partner exceeded the time spent with any nonpartner for 90% of birds. The preference value of the partner during the year preceding first nesting was comparable to the amount of time spent with the partner in the year following first nesting, demonstrating the uniqueness of associations between future breeding pairs.

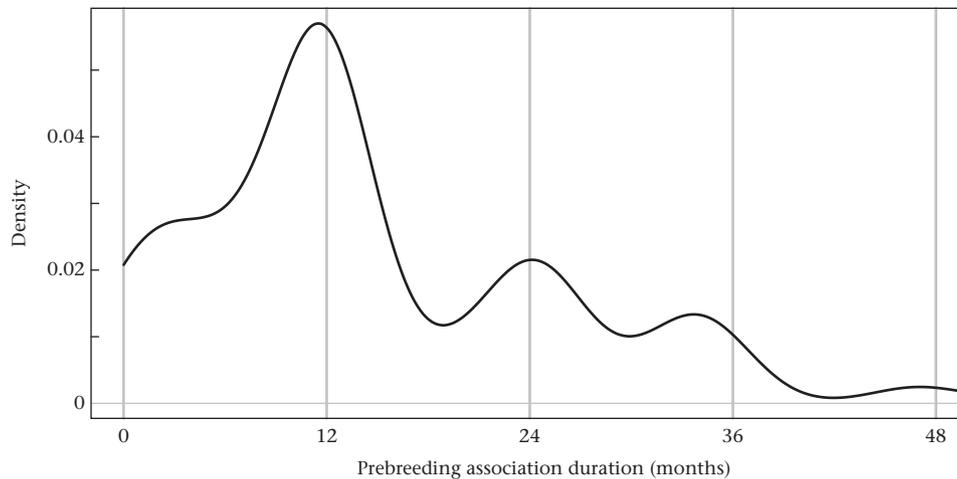


Figure 2. Time between pair association and first breeding. The prebreeding association duration is the number of months between the first association of the pair (i.e. the beginning of the period during which a pair was first seen together for at least three consecutive months) and the first date their nest was recorded. Vertical grey bars are at 0, 1, 2 and 3 years before first breeding. Notice peaks at 12 months and 24 months before first breeding.

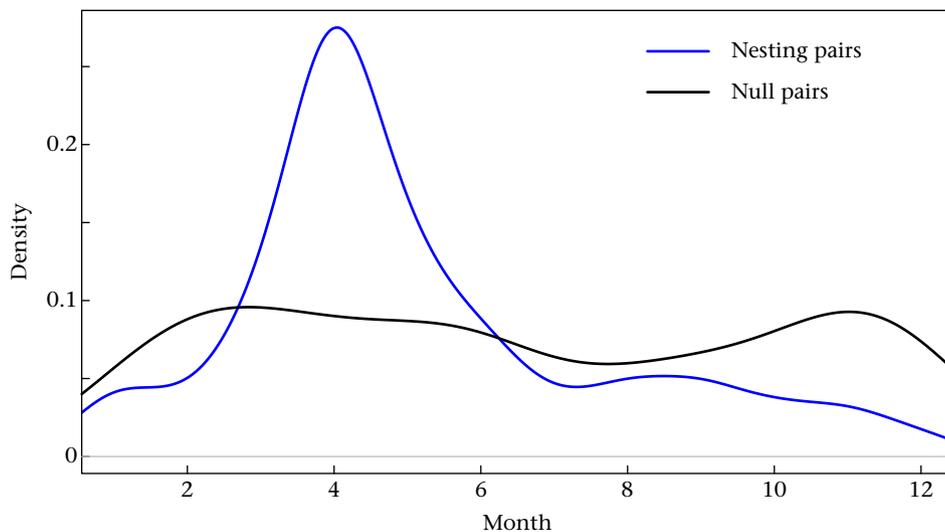


Figure 3. Month of first associations. The month indicates the month in which a pair began associating (i.e. the beginning of the period when a pair was seen together for at least three consecutive months). The blue line shows birds that eventually became breeding pairs and peaks in late spring, the time at which whooping cranes arrive on their breeding grounds. Ninety-eight per cent (57/58) of breeding pairs associated for at least three consecutive months prior to breeding. Null pairs represent potential pairs, which are male/female duos that could have become breeding pairs but did not (for detailed definition see Methods). Only 13% of null pairs associated for at least three consecutive months and for those that did so, there was no trend in the month in which these null pairs formed (black line).

sexual maturity is considered to be at least 3 years in this species (Archibald & Lewis, 1996; Travsky & Beauvais, 2004; Urbanek & Lewis, 2015), but we found that 60% (SE = 54–67%) of pairs began associating before at least one partner was 3 years old and 21% (SE = 15–26%) of pairs began associating before either partner was 3 years old. These early associations with a future partner may provide direct benefits to juveniles, since being a member of a pair can provide a competitive advantage (e.g. in corvids: Emery et al., 2007), resulting in an increase in social status (Black, 2001; Emery et al., 2007; Kraaijeveld, Gregurke, Hall, Komdeur, & Mulder, 2004; Paulus, 1983; Poisbleau et al., 2006). Observations of wild migratory cranes indicate that at least some pairs are territorial on both the breeding and wintering grounds (Allen, 1952; Alonso, Bautista, & Alonso, 2004) and pairs become more dominant with time (Stehn, 1992), so early-life association may allow birds to acquire high-quality territories and more resources. Furthermore, studies of divorce suggest that survival is higher for

paired birds (Nicolai et al., 2012; Servanty et al., 2014), possibly because of mutual protection from predation (Nicolai et al., 2012). Thus, by beginning to associate even before sexual maturity, juvenile whooping cranes may gain social status, territory, resources and/or protection.

In addition to directly benefitting juveniles, early association between pair members could allow partners to become familiar with one another even before beginning breeding. Numerous studies point to a positive relationship between pair familiarity and breeding success independent of individual breeding experience, possibly via increased hormonal or behavioural compatibility over time (Angelier et al., 2007; Laubu et al., 2016; Ouyang et al., 2014) or improved coordination in feeding and guarding behaviour (Sánchez-Macouzet et al., 2014). Whether these mechanisms operate even before a pair begins breeding has not been described, but barnacle geese, *Branta leucopsis*, do eventually pair with associates from early in life and show increased reproductive success

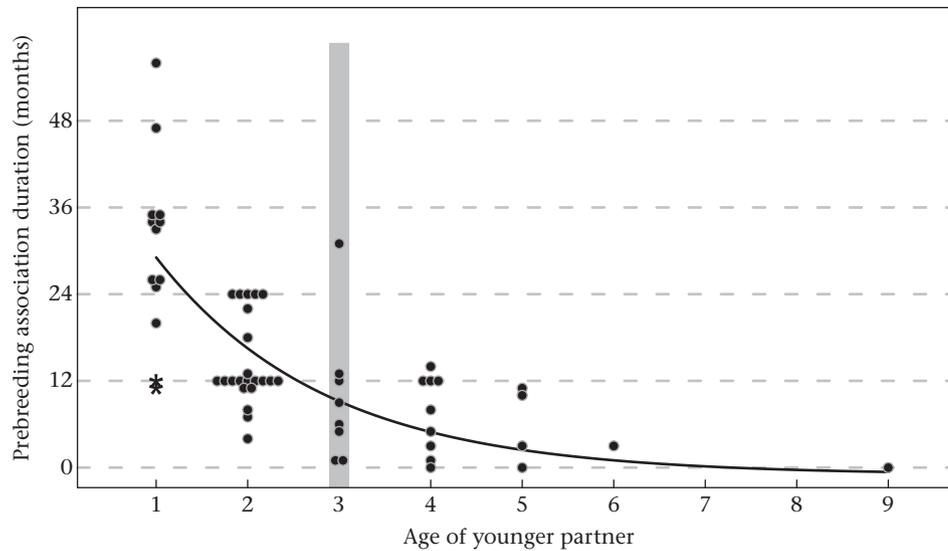


Figure 4. Prebreeding association duration decreases with the age of birds in a pair. The curve displays predictions from a generalized linear model predicting prebreeding association duration from the age of the younger member in a pair. The vertical grey bar shows the nominal age of sexual maturity; a large proportion of pairs (60%, SE = 54–67%) began associating when at least one partner had not yet reached sexual maturity. The significant negative relationship between prebreeding association duration and age is driven partly by the formation of a number of pairs before one partner had reached sexual maturity. Still, even in cases where both partners had reached sexual maturity, the prenesting bond duration was greater than zero months in the majority of cases. All ages are integers; the spread of points within each age group is for visualization only. Points shown as asterisks are the two cases in which a pair attempted to breed when one of the partners was 2 years old; in both cases, eggs were infertile.

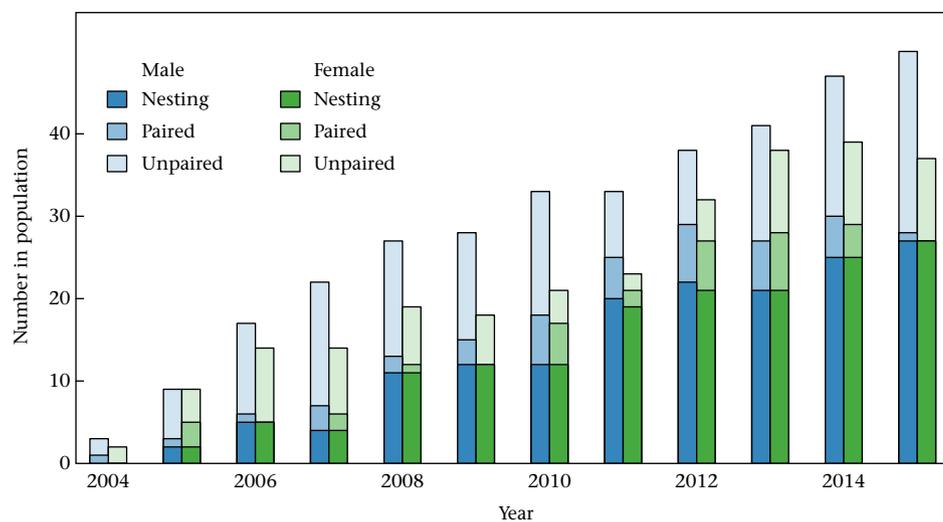


Figure 5. Unpaired and non-nesting birds of reproductive age are present in the population during the breeding season. During any year, there were individuals of both sexes that were unpaired. Darker bars show individuals that were paired but did not nest; most individuals that were paired but did not nest were 3–4 years old. Mismatches between the numbers of paired birds of each sex in 2011 and 2012 are due to pairings involving birds younger than 3 years old.

with longer pair bonds (Black et al., 1996; Choudhury & Black, 1994), suggesting that early-life familiarity may result in higher breeding success. Similarly, some pairs of bearded reedlings, *Panurus biarmicus*, that practise nesting behaviours during the prebreeding period have higher nesting success at their first attempt than to those who do not practise nesting (Griggio & Hoi, 2011). Similarly, we saw two instances where whooping cranes paired when one partner was 1 year old and then nested at age 2; in both cases, eggs were infertile, and there are no records of a 2-year-old whooping crane producing fertile eggs, but even without successful reproduction, this premature nesting could be beneficial if it improves the probability of success in future breeding attempts. By beginning to associate early in life and maintaining these

associations until the time of breeding, whooping cranes may be able to combine the social advantages of juvenile partnerships and the breeding benefits of partner familiarity.

One possible alternative driver of the patterns in prebreeding associations we detect here could be mate-guarding behaviour. Mate guarding is not a mutually beneficial behaviour; males gain an advantage because they secure a future breeding partner or retain an existing mate, but females do not necessarily benefit (Slatyer, Jennions, & Backwell, 2012). However, since we lack behavioural observations we could not assess whether mate guarding was an important driver of these association patterns. In addition, although we saw early-life associations between pair members in this population, early formation of pair bonds could be limited by

other factors, including hormonal and physiological constraints (Soares et al., 2010), so the absence of these early associations in other monogamous species does not necessarily indicate a lack of potential benefit.

When examining the sex ratio and presence of unpaired birds in this population, we found little evidence that whooping cranes experience high divorce costs from competition for mates. The sex ratio of sexually mature birds was slightly male-skewed, and three of seven divorces were followed by re-pairing by the female but not by the male partner, both of which would be consistent with a high cost of partner loss for males (Harts & Kokko, 2013). However, there was a considerable number of unpaired sexually mature birds of both sexes in the population, which means that mates were available to the unpaired males, and most unpaired or nonbreeding birds found a partner within 1 year. Especially given that during the study period the population shared one small breeding area, it is unlikely that whooping cranes have difficulty finding an available mate following divorce, but it is conceivable that these unpaired birds are considered low-quality mates or are in an endocrine state that is unsuitable for breeding (Bluhm, 1988; Dittami & Reyer, 1984). The presence of nonbreeding individuals has been previously reported in whooping cranes (Allen, 1952); in other species, nonbreeding adults are those who failed to maintain territories (Nesbitt, 1989) or have low body condition following adverse winter conditions (Tryjanowski, Sparks, Ptaszyk, & Kosicki, 2004), which are possible in this population as well. Furthermore, as the population grows and expands its breeding area (WCEP, 2016), there is the potential for segregation where not all unpaired individuals are available to one another, possibly creating more unpaired sexually mature birds. Although our data suggest that finding a mate would be possible following divorce in this population, there are additional potential drivers of high divorce costs not addressed by our analyses, including high energy requirements of courtship or hormonal limitations to pairing. Thus, divorce costs may still play a role in driving monogamy in whooping cranes, possibly synergistically with the benefits conferred by pair associations.

Breeding success in this population of whooping cranes is very low and largely driven by environmental factors, including the presence of blood-feeding black flies (Converse et al., 2013; Runge, Converse, & Lyons, 2011; Servanty et al., 2014; Urbanek, Zimorski, et al., 2010). This low reproductive success at first breeding means that we were unable to examine the effect of prebreeding associations on eventual breeding success. However, in other species, nesting success can be related to pair bond duration (Black et al., 1996; Leu, Burzacott, Whiting, & Bull, 2015; Liu, He, Kuang, & Xue, 2010; Sánchez-Macouzet et al., 2014), and many of the proposed mechanisms for this relationship apply to prebreeding pair associations as well (e.g. hormonal or behavioural convergence). Pair familiarity can also help birds cope with severe environmental conditions (Gabriel & Black, 2013; Lewis et al., 2009), suggesting that the breeding behaviour of this population may change as pairs behaviourally adapt to the conditions at their breeding grounds.

In contrast to previous studies, which focused on the wintering grounds (Owen et al., 1988; Stehn, 1992), we found that the majority of pairs began associating in early spring, at the time of arrival on the breeding grounds. In this population, the spatial extent of the summer range is much smaller than the winter range (Teitelbaum et al., 2016), creating more opportunities for social interaction and mate selection during that time of year (Bluhm, 1988), provided birds are in an appropriate endocrine state for pairing (Soares et al., 2010). Based on our study of a single population, we cannot necessarily generalize the finding that pairs begin associating on the breeding grounds, but our results highlight the

importance of considering year-round interactions when studying mating systems. In addition, future research into the effects of juvenile associations in annually monogamous species and nonpairs would help resolve questions about the social and reproductive benefits of prebreeding associations. Here, we show that association between pair members in a long-term monogamous species occurs over a long period before breeding and may confer direct benefits in addition to those gained from breeding itself; future studies should take into account the behaviour of pairs prior to breeding.

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Supplementary material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2017.10.015>.

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