



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

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