



Difference in arrival date at the breeding site between former pair members predicts divorce in blue tits



Carol Gilsenan, Mihai Valcu, Bart Kempenaers*

Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Seewiesen, Germany

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Divorce occurs when both members of a breeding pair survive to the following year but then pair with other individuals instead of reuniting. Divorce is common in birds, but its frequency can vary widely both between and within species, or even between populations across years. Several explanations for divorce have been described, both adaptive and nonadaptive. Many studies have compared the breeding success of faithful and divorced individuals, but fewer have considered the process of divorce, i.e. the events that lead up to divorce. In this study, we used data from eight breeding seasons to investigate divorce in a population of blue tits, *Cyanistes caeruleus*, in southern Germany. To compare our results to previous work, we first describe the frequency of divorce and compare the breeding success of divorced and faithful pairs. We then use data from an RFID transponder-based system, where all visits of individuals to any nestbox in the study site are automatically recorded throughout the year, to compare the behaviour of pairs in the interbreeding period. We found that the probability of divorce was not affected by breeding success in Year X. However, divorce was predicted by the difference in arrival time to the study site between the members of Year X pairs. Furthermore, during the interbreeding period, compared to their divorced counterparts, members of faithful pairs had more interactions with one another than with other individuals of the opposite sex. In Year X + 1, faithful females started egg laying earlier, had somewhat larger clutches and produced slightly more fledglings, than females that had divorced. We propose that divorce in blue tits is a by-product of separation of the two pair members after the Year X breeding season, leading to asynchrony in the timing of settlement and pair formation in Year X + 1.

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Divorce, where one or both individuals from a previous breeding pair form a new pair with another individual while their former partner is still alive (Coulson, 1972), occurs in many bird species (see review in Black, 1996). The probability of divorce depends not only on individual life histories, but also on extrinsic factors such as breeding site quality (e.g. Blondel, Perret, & Galan, 2000). Consequently, the rate of divorce can vary widely between species (see reviews in Rowley, 1983; Ens, Choudhury, & Black, 1996), and even between populations of the same species (e.g. Dhondt & Adriaensen, 1994).

In general, remaining faithful to a mate from one breeding season to the next can provide several advantages to an individual (see reviews in Rowley, 1983; Culina, Radersma, & Sheldon, 2014).

Reuniting or staying with a mate across multiple years means less time and energy will be spent in finding a new mate and establishing a new pair bond (Bried & Jouventin, 2001), or in exploring an unfamiliar territory (Black, 1996) if divorce coincides with moving to a new breeding site. Newly formed pairs may also be less efficient than faithful pairs in coordinating breeding and parental behaviours (e.g. feeding offspring). Ultimately, mate fidelity may lead to higher reproductive success. Indeed, it has been shown that females of faithful pairs start laying earlier in the season (see review in Rowley, 1983), and that faithful pairs fledge more young than pairs containing divorced individuals (Dhondt, 2002; Diamond, 1987).

If mate fidelity leads to higher fitness why, then, are cases of divorce frequently observed in populations? One set of hypotheses suggests that divorce is adaptive for at least one member of a pair; individuals should divorce when the benefits outweigh the costs of mate change (Choudhury, 1995). Evidence that divorce might be adaptive comes from studies showing that at least one member of a divorced pair improves its reproductive success (Dhondt &

* Correspondence: B. Kempenaers, Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, E. Gwinnerstr, 82319 Seewiesen, Germany.

E-mail address: b.kempenaers@orn.mpg.de (B. Kempenaers).

Adriaensen, 1994; Green, Krebs, & Cockburn, 2004; Linden, 1991; Marzluff, Woolfenden, Fitzpatrick, & Balda, 1996; Orell, Rytkönen, & Koivula, 1994; Ramsay, Otter, Mennill, Ratcliffe, & Boag, 2000; Streif & Rasa, 2001). The underlying reasons for improved breeding success may be diverse, but can be summarized as obtaining a higher quality territory (Desrochers & Magrath, 1996; Blondel et al., 2000; the 'habitat-mediated' hypothesis, Newton & Wyllie, 1996), a higher quality mate (where females may use male quality indicator traits to make decisions about divorce, e.g. body size or ornaments: Ryan, 1998; individual rank in a flock: Otter & Ratcliffe, 1996) or a more compatible mate (the 'incompatibility' hypothesis, Coulson, 1966; Coulson & Thomas, 1980), where 'incompatibility' can be genetic or behavioural (see Ihle, Kempenaers, & Forstmeier, 2015). In general, this is referred to as the 'better option' hypothesis (Ens, Safriel, & Harris, 1993). Thus, divorce might be a mechanism to remedy the costs of having mated with a genetically related mate ('inbreeding avoidance'; Kempenaers, Adriaensen, & Dhondt, 1998; Hatchwell, Russell, Ross, & Fowlie, 2000), a less fertile or infertile mate (see Hasson & Stone, 2009 for a mathematical model that predicts an increase in female infidelity as a response to certain aspects of male infertility) or an unfaithful mate (higher risk of paternity loss for a male; Cézilly & Nager, 1995).

The observation that one or both former pair members increase their fitness after a divorce can erroneously be taken as evidence that divorce is an active behavioural 'decision' of at least one pair member. Divorce might also be the consequence of other processes that do not involve a decision to leave the previous partner. For example, strong intrasexual conflict for access to a potential mate can lead to a new male or female taking over a territory/mate, with passive acceptance of the usurper as the new breeding partner (Daniels & Walters, 2000; Heg, Bruinzeel, & Ens, 2003; Taborsky & Taborsky, 1999; Valcu & Kempenaers, 2008). Divorce may also occur because of timing differences in arrival and settlement of previous pair members ('musical chairs' hypothesis, Dhondt & Adriaensen, 1994) simply because of separation during the nonbreeding season ('accidental loss' hypothesis, Owen, Black, & Liber, 1988). An individual may then decide to pair with a new partner rather than wait, possibly in vain, for their previous partner to return (Gonzalez-Solis, Becker, & Wendeln, 1999). In these contexts, divorce could even be maladaptive for both members of the previous pair, that is, both could have a lower breeding success after the separation.

Most studies on divorce in birds have focused on the differences in reproductive success or on between-year changes in fitness measures between faithful and divorced pairs (see meta-analyses in Dubois & Cézilly, 2002; Culina et al., 2014). However, as explained above, the results of such studies are not sufficient to conclude that divorce is an adaptive mating tactic. The specific behaviours of individuals in between breeding attempts that may ultimately lead to divorce remain relatively poorly studied, even though this is necessary to understand how and why divorce occurs in a population.

We studied divorce in a nestbox-breeding population of blue tits, *Cyanistes caeruleus*, in southern Germany. The blue tit is a small secondary cavity-nesting passerine species that is common throughout most of Europe. Most blue tits are socially monogamous with biparental care and produce one clutch per pair per breeding season (Perrins, 1979). The proportion of pairs that divorce ranges from 8% to 85% between populations (Dhondt & Adriaensen, 1994). The general aim of our study was to investigate whether divorce is an active choice (a mating tactic) employed by at least one pair member or whether it is a passive outcome of intrasexual competition or behaviour during the nonbreeding season. First, we investigated whether aspects of a pair's

reproductive success (lay date, clutch size and fledging success) in Year X can predict divorce in Year X + 1. Second, we tested whether reproductive success differs between males and females from faithful pairs and those that divorced (Year X + 1), and we compare our results with those from the literature. Third, we analyse spatiotemporal patterns of the presence of individuals at nestboxes between winter and the start of breeding to gain insight into the behavioural mechanisms behind divorce. A previous study (Valcu & Kempenaers, 2008) suggested that divorce may be the consequence of female–female competition. If intrasexual conflict over a mate or breeding territory is the main cause of divorce, we expected to see visits to the future breeding nestbox by at least two competing same-sex individuals. We also report when both members of a new or faithful pair first visited the future breeding nestbox (or any nestbox), providing insight into the timing of territory establishment or pair formation.

METHODS

Study Site

This research was carried out as part of a long-term study on the reproductive biology of a blue tit population in a protected forest site in southern Germany. The study area ('Westerholz', 48°08'26"N, 10°53'29"E) is a 40 ha mixed deciduous/coniferous forest equipped with 277 nestboxes since 2007 to monitor breeding (converted to 'smart' nestboxes, hereafter 'SNBs', in 2009; see Schlicht, Grg, Loës, Valcu, & Kempenaers, 2012 for more details). Each year, the breeding population consists of between 60 and 100 blue tit pairs.

Field Procedures

On four occasions during each winter (in the first week of November, December, January and February), roosting individuals were caught inside the nestboxes at night. During the breeding season, adults were caught in the nestbox, using an automated trapping system or by hand, when they fed 8–10-day-old nestlings. Unbanded birds were ringed with a unique combination of one metal band and three plastic colour bands, and a blood sample (ca. 50 µl) from the brachial vein was taken for molecular sexing and parentage analysis. Each individual was measured (tarsus and third primary wing feather ± 0.5 mm, weight ± 0.1 g), and age (yearling or adult) and sex were determined based on plumage characteristics. New birds were also implanted with a passive integrated transponder, which allowed them to be uniquely identified by the SNBs (see Schlicht et al., 2012 and below for more details).

During the breeding season (from early March until early June), each nestbox was visited at least weekly to check for presence of nesting material. When a nest had reached a 'lining' stage (i.e. a completed nest lined with feathers or other soft material), it was checked daily to determine the date the first egg was laid (hereafter 'lay date'). Weekly checks thereafter allowed us to determine clutch size. Towards the end of incubation, around 2 weeks after clutch completion, nestboxes were checked daily again to determine hatch date. The number of young in each nest were counted at least every week until fledging.

Smart Nestbox Data Collection

Each nestbox was fitted with a transponder reader and with two light barriers, one at the inside, and one at the outside of the entrance hole (see Schlicht et al., 2012 for technical details), such that all entries and exits of birds (with transponder number, if available) were recorded with date and time (based on real-time

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