With or without you – pair fidelity and divorce in monogamous birds

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Abstract

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The drivers of fidelity and divorce of pair-bonded individuals, along with their fitness consequences, are of great interest as they influence mating systems, population structure and productivity, and gene flow. Socially monogamous birds offer an ideal opportunity to study divorce since they show great variability in the extent to which pair bonds are maintained. However, there has been little consensus as to whether divorce is a behavioural adaptation to improve a mating situation, or a consequence of other processes. Moreover, the biological and ecological correlates of fidelity are difficult to address because previous work has been based on indirect and potentially biased methods. Finally, in terms of process, the link between the process of mate choice and subsequent mating decisions has been largely inaccessible to study.

My doctoral thesis addressed these significant gaps in our understanding of cause, process and consequence in the formation and dissolution of pair bonds in socially monogamous birds. I accomplished this in three principal ways. First, I conducted a robust phylogenetic meta-analysis on 84 studies across 64 species to assess the existing empirical evidence that divorce in socially monogamous birds is adaptive (in terms of breeding success). This analysis revealed that divorce is, in general, adaptive as it is both triggered by relatively low breeding success and leads to improvement in success.

Next, I developed a novel probabilistic multievent capture–mark–recapture framework that provides joint estimates of survival and fidelity while explicitly accounting for imperfect detection, capture heterogeneity, and uncertainty in pair status. By applying this model to breeding data on a wild great tit population I showed that birds that remain faithful to their partner exhibit higher survival rates and are more likely to remain faithful in the next breeding season than do birds that change partners. Subsequently, I confirmed the generality of a survival benefit by applying the model to breeding data on other tit populations. Then, by applying the model to data from a population of mute swans, I showed that fidelity decreases the likelihood of skipping breeding and mortality in this long-lived species, and that these effects depended on age, individual quality, and immigration status.

Finally, I investigated how the timing of pair formation influences breeding success and divorce probability using five years of data on the over-winter social behaviour of great tits. I showed that early pair formation had a positive effect on fitness components, influencing the likelihood of divorce only indirectly, through breeding success. Further, my work revealed that males, but not females, with higher numbers of the female associates in winter, and males whose future breeding partners were ranked low amongst these, divorced more often.

My research makes a significant contribution to our understanding of divorce and fidelity, and generates a number of important implications for future studies. First, my work establishes that divorce is adaptive for breeding success. Second, my results highlight that survival is an important (and likely, widespread) fitness consequence of pairing decisions. Third, I provide a novel statistically rigorous modelling framework for estimating fidelity-rates and testing hypothesis about fidelity that overcomes many of the inherent biases in traditional estimates. Fourth, it provides the first evidence for a selective advantage of early pair formation in wild, thus highlighting that there are benefits to pair familiarity that manifest via social associations of individuals prior to breeding. Finally, my work reveals the selective pressures operating via the social environment can ultimately influence the mating strategies individuals adopt.

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Author Contributions

Main contributors

Antica Culina had independent input into all aspects of this thesis, and contributed to all EGI-collected data (spring breeding season ringing and winter social network). Also, analysed data, wrote first drafts, and incorporated co-author comments to produce final manuscripts.

Ben C. Sheldon (supervisor and co-author of Chapters 2, 3, 4, 5, 6, 7) secured funding, provided intellectual input, guidance on data analysis, and gave comments on all chapters.

Camilla A. Hinde (co-supervisor and co-author of Chapters 6, 7) had intellectual input and provided detailed comments on all co-authored chapter drafts. Provided comments on Chapters 1 and 8.

Shelly Lachish (co-supervisor and co-author of Chapters 3, 4) had intellectual input, provided guidance on data analysis and detailed comments on all co-authored chapter drafts.

Additional contributors

Reinder Radersma (co-author of Chapter 2) had intellectual input, provided guidance on data analysis and detailed comments on the co-authored chapter draft.

Roger Pradel (co-author of Chapter 3) provided guidance on data analysis and detailed comments on the co-authored chapter draft.

Remi Choquet (co-author of Chapter 3) provided guidance on data analysis and detailed comments on the co-authored chapter draft.

Chris M. Perrins (co-author of Chapter 5) collected the data, and provided detailed input on the population processes in the studied population.

Contents

CHAPTER 1

Introduction

Introduction

Social monogamy is defined as a mating system in which there is apparent co-operation of one male and one female in breeding for the duration of at least one breeding attempt, without any assumptions about exclusivity of copulation between them (reviewed in Choudhury 1995, Black 1996). The need for the term 'social monogamy' appeared when it was recognised that many species previously simply classified as being 'monogamous' were not indeed genetically monogamous. These genetic mating patterns are commonly described through the patterns of extra-pair paternity (i.e. infidelity), where extra-pair copulations occur at the same time as the social partnership persists (i.e. within the same breeding season/event). The other axis that describes variation in the genetic mating pattern is determined by the partnership's stability over the lifetime of individuals. Social monogamy can in this way be described from being serial to permanent (often termed as short- and long-term partnerships). The majority of studies of social monogamy in animals concentrate on birds, as this is the predominant mating system in the group, with more than 95% of species being socially monogamous (Lack 1968, Bennett and Owens 2002), compared with, for example, only 9% of mammal species (Lukas and Clutton-Brock 2013). One of the main explanations for this quite pronounced difference between birds and mammals is that, unlike in mammals (where placentation is internal, and only the female lactates), male birds make a substantial contribution to parental care (Lack 1968).

The interaction between costs and benefits of offspring (or mate) desertion (in terms of offspring survival, and options to acquire a new mate) rather than the costs alone or the benefits alone will determine the likelihood of desertion, and thus the appearance of alternative mating strategies (i.e. social and genetic mating system) at the species, population, or individual level (Bennett and Owens 2002). Accordingly, the hierarchical view of the evolution of the avian mating systems (Bennett and Owens 2002) is that: (i) life-history of a species determines whether desertion of a brood is possible (i.e. parental care of only one parent is sufficient to successfully raise offspring); (ii) ecological conditions determine whether desertion is viable in a species or a population; (iii) social interactions determine whether the strategy will be adopted by a particular individual.

While social monogamy is present in almost all bird species, long-term partnerships, defined as the maintenance of the pair bond in subsequent breeding seasons, are much less widespread (21% of the 159 bird families, Black 1996). Individuals that survive between two subsequent breeding seasons may remain faithful to their previous partner or may change partner. If they change partner they may do so because their previous partner has died (i.e. widowing), or they may 'divorce' the partner (while the partner is still alive) either by choice or by necessity (because they themselves have been left by the partner, or because of accidental separation). Divorce has been recorded in 92% of socially monogamous birds (Jeschke and Kokko 2008), with divorce rates being highly variable both among and within species. For example, divorce has almost never been observed in the red-billed chough, *Pyrrhocorax pyrrhocorax* (Banda and Blanco 2014), while nearly all pairs of the house martin, *Delichon urbica*, divorce (Bryant 1979). Divorce rates may also vary considerably among populations of the same species (e.g. 8% - 85% in the blue tit, *Parus caeruleus*, Dhondt and Adriaensen 1994). What causes this variation in fidelity and divorce rates? What are the underlying factors predisposing a species or a population, as well as individuals within a population, to a certain level of maintenance or dissolution of pair bonds?

Work towards answering these complex questions can greatly increase our understanding of the evolution of social monogamy and long-term partnership, as well as its broader consequences (reviewed in Black 1996, Reichard and Boesch 2003, Shuster and Wade 2003). Moreover, if divorce is considered as a component of mate choice (Birkhead and Moller 1996, Black 1996, Dubois et al. 1998), where one or both pair members choose not to mate with the former partner again, it might well be argued that divorce plays a role in the process of sexual selection (Diamond 1987).

One potential approach towards understanding the causes and consequences of apparent differences in rates of fidelity and divorce in monogamous birds can be similar to the approach taken to understand the appearance of social mating systems (Bennett and Owens 2002). Consider a three-tiered hierarchy: (i) at the level of a species, life-history will determine constraints on the costs and benefits of fidelity and divorce; (ii) at the population level, ecological and demographic factors (which not only vary between populations but also temporarily within a population) will further shape these costs and benefits; (iii) at the level of an individual, the social interactions it has with other conspecifics and its own traits will determine whether staying with a partner or divorcing it is possible and/or beneficial for that individual.

Fitness costs and benefits of mate fidelity and divorce

At the functional level, the costs and benefits of fidelity and divorce are those of fitness (i.e. survival and reproduction) with the benefits of one option often being the costs of the other (reviewed in Black 1996). The fitness benefits of remating with the same partner are most often viewed in terms of reproductive benefits (i.e. increased breeding success). A number of empirical studies have supported the hypothesis that staying with the same partner leads to higher breeding success (e.g. Perrins and McCleery 1985, Bradley et al. 1995, Rees et al. 1996, Pyle et al. 2001, Wiktander et al. 2001). These reproductive benefits can come about through the so-called 'mate familiarity effect' (Tinbergen 1959, Black 1996, Black 2001), or through benefits not directly related to the familiarity *per se*. For example, birds that stay faithful to their partner avoid the risk of skipped breeding if a new partner is not acquired (e.g. Ens et al. 1993, Taborsky and Taborsky 1999). Moreover, already paired birds might experience the advantages of an earlier onset of breeding (e.g. Verhulst and Tinbergen 1991, Van de Casteele et al. 2003), as they need not spend time establishing a new partnership (Lifjeld and Slagsvold 1988, McGraw and Hill 2004, Pampus et al. 2005). The 'mate familiarity effect' acts through improved coordination, cooperation and responsiveness between familiar pair members

(Hirschenhauser et al. 1999, Weiss et al. 2010). For example, familiar birds, in comparison to the ones in new partnerships, may be better coordinated in their parental activities as well as more competitive in the acquisition of a nest site and food for the brood (e.g. Brooke 1978, Cooke et al. 1981, Choudhury and Black 1994, Fowler 1995; but see Hatch and Westneat 2008).

The second component of fitness, survival, is less often considered in the studies on fitness consequences of fidelity and partner change. Survival over winter, which is the period of the highest mortality in many bird species (Lehikoinen 1987, Haftorn 1989, Houston and McNamara 1993, Gosler 2002, Koivula et al. 2002), greatly impacts overall (i.e. lifetime) fitness. There are two main ways in which pair status may affect winter survival. First, the benefical effects of breeding with a familiar partner (e.g. if due to better coordination of pair members less energy is spent during the breeding season) likely lead to better body condition at the begining of the winter, and consequently to higher winter survival. Second, in species where males and females spend winter in mixed-sex flocks, paired birds may experience enhanced survival as a result of better access paired individuals have to limited resources (e.g. food, roosting sites), as has been shown for the barnacle goose, *Branta leucopsis* (Black et al. 1996). Paired birds might also benefit from shared anti-predator behaviours (e.g. male willow tits, *Poecile montanus,* produced anti-predator alarm calls more frequently when their female was nearby, Hogstad 1995). Moreover, in species where winter survival is related to social status, individuals may benefit by remaining with a dominant partner (Ekman 1990, Lemmon et al. 1997). Finally, birds that stay in an already established partnership experience improved survival if they avoid costs associated with searching for a new partner (Choudhury 1995, Black 1996).

Partner fidelity can be also costly. First, there are costs associated with failure to reach full reproductive potential due to being paired with an incompatible partner (Coulson 1966, 1972), or a partner of low quality (Ens et al. 1993), as well as potential costs of reduced genetic diversity of the offspring. The only way that individuals of socially monogamous species with bi-parental care can correct for suboptimal partnerships, or increase the genetic diversity of offspring, is through secondary mating strategies: infidelity and divorce. In this case, changing a partner can lead to an increase in breeding success (Culina et al. 2014: Chapter 2). Second, there are costs associated with the maintenance of contact with the mate (in continuous partnerships), and costs related to waiting for a mate, who might be dead, to return (in part-time partnerships). In the latter case, waiting might incur costs of not finding a new breeding partner, or of not finding a good new breeding partner.

Influence of life-history traits and demographic factors on pair-bond dynamics

Fitness costs and benefits of remating and divorce in socially monogamous species will be shaped at the 'higher' hierarchical levels by the life-history of the species (Rowley 1983, Jouvetin and Bried 2001, Bried et al. 2003) and the ecological and demographic factors a population is exposed to (Ens et al. 1993, Dhondt et al. 1996, Marzluff et al. 1996, Bried and Jouventin 1999, Maness and Anderson 2007). These factors impose the upper and lower limits to the way breeding success and survival can be affected by different mating outcomes, and contribute to the species- and population-specific differences in the rates at which pair bonds are maintained. Consequently, studies trying to understand the drivers of the differences in pair fidelity and divorce rates use species- or population-specific factors and relate them (in comparative analyses) to observed rates of pair fidelity and divorce (Dhondt et al. 1996, Cezilly and Zayan 2000, Bried et al. 2003, Maness and Anderson 2007, Liker et al. 2014).

Life-history traits that have been found to correlate with divorce rates of monogamous species include longevity, continuity of partnership (i.e. whether pair members stay paired between the two breeding seasons or not), breeding site fidelity, and the degree of coloniality. The majority of empirical evidence supported the hypothesis that divorce rates are higher in short-lived compared to long-lived species. Bried et al. (2003) detected an overall positive relationship between adult life expectancy and mate fidelity in Procellariiformes (albatrosses and petrels), and several other studies found that species with higher average mortality also exhibit higher average divorce rates (Cezilly et al. 2000, Jeschke and Kokko 2008, Botero and Rubenstein 2012). However, there are exceptions to this general pattern. For example, some long-lived species (e.g. flightless cormorants, *Nannopterum harrisi*, Harris 1979, greater flamingos, *Phoenicopterus ruber*, Cezilly and Johnson 1995) show high divorce rates, while some short-lived species (e.g. zebra finch, *Taeniopygia guttata*, Zann 1994) show very low divorce rates.

Species that form part-time partnerships (i.e. sexes spend winter separately, these are mostly migratory species) tend to have higher divorce rates than species with continuous partnerships, as supported by several comparative analyses (Jeschke and Kokko 2008, Botero and Rubenstein 2012, Liker et al. 2014). In species with part-time partnerships, the costs of waiting for the former mate to return (i.e. delayed breeding, skipped breeding), while the latter might be dead, are likely to outweigh the benefits of fidelity or the costs of search for a new partner (Bried and Jouventin 2002). Divorce rates are also generally found to be higher in colonial than in non-colonial species (Dubois et al. 1998, Jeschke and Kokko 2008, Liker et al. 2014); however, the trend is not always detected (Botero and Rubenstein 2012). The likely reason behind this pattern is simple: birds breeding in colonies have more opportunities to sample and evaluate a large number of future potential partners. There is a relatively widely supported view that fidelity to a mate should correlate positively with the site fidelity (Rowley 1983, Pietz and Parmelee 1994, Aebischer et al. 1995, Cezilly and Zayan 2000). However, two comprehensive comparative analyses came to different conclusions: while the correlation between site fidelity and mate fidelity in Ciconiiformes was positive (Cezilly et al. 2000), there was no correlation between the two in Procellariiformes (Bried et al. 2003).

At the population level ecological and demographic factors will influence the number, variability and quality of potential partners, and further shape the costs and benefits of fidelity and partner change. For example, changes in mortality within the same population may not only lead to lower rates of pair fidelity through widowing, but also through new breeding vacancies becoming available after one partner dies, especially if certain types of individuals are more likely to die. For example, Ens et al. (1993) have found that due to the selective mortality of the individuals of a lower quality, divorce rates increase with mortality rates in an oystercatcher (*Haematopus ostralegus*) population as more individuals of a higher quality become available. Age structure and adult sex ratios have also been found to correlate with divorce rates: divorce rates in the population of barnacle geese increased with an increased proportion of more experienced, older individuals amongst the unpaired birds (Black et al. 1996). Finally, across bird species divorce rates have shown to be higher in populations with female biased sex ratios (Liker et al. 2014).

Individual social interactions and divorce

Most of the studies on the causes and consequences of divorce and fidelity focus on the general patterns observed at the population level. However, population level patterns rarely provide the comprehensive insights into processes happening at the individual level and at the finer time-scale (i.e. between two breeding seasons). For example, the ‘success-stay/failure-leave’ pattern (Schmidt 2004) is often observed at the population level, where those pairs that fail (i.e. have low breeding success) divorce, and those that succeed stay together. However, some pairs stay together after a failure, while others divorce after a successful breeding attempt (e.g Brooke 1978 for manx shearwater, *Puffinus puffinus*, Harris et al. 1987 for oystercatcher, Jones and Montgomerie 1991 for least auklet, *Aethia pusilla*, Ramsay et al. 2000 for black-capped chickadees, *Poecile atricapillus*, Saino et al. 2002 for barn swallow, *Hirundo rustica*). This suggests that an individual’s decision-making might be constrained by its social interactions, and/or that population consists of individuals with different strategies regarding when and whether to divorce their partner (Naves et al. 2006).

With the establishment of the use of social network theory to study heterogeneous associations within animal groups, describing how individuals differ in their social interactions (social network traits of individuals) has become much easier and more straightforward (reviewed in Croft et al. 2008, Sih et al. 2009, Kurvers et al. 2014). There is increasing evidence that the social environment individuals are exposed to influences their fitness and overall population dynamics (McDonald 2007, Ryder et al. 2008, Oh and Badyaev 2010, Kurvers et al. 2014). One example is a study on mating success of male house finches, *Carpodacus mexicanus*. Oh and Badyaev (2010) have shown that males possessing one of two combinations of morphological and social network traits have the highest mating success. Males with highly elaborated ornamental traits (shown to be preferred by females) but with low betweeness-centrality (a social network measure that reflects how often a male changed wintering flocks) had the same mating success as males on the lowest spectrum of the ornamental elaboration but with the highest betweeness-centrality. Just as the social network position of an individual might influence pair formation, the social network position of individuals might also make them more prone to divorce their partners, or to be divorced themselves. Finally, if divorce is an active decision of at least one of the pair members (Choudhury 1995), we expect it to be influenced by the availability of unpaired individuals in the population (Ens et al. 1993, McNamara et al. 1999, Maxin and Berec 2010) as well as the opportunity for a focal individual to interact with them (and, consequently, assess them as potential new partners), given that social interactions and associations among members of a population are almost never homogeneous (Krause et al. 2007, Wey et al. 2008, Sih et al. 2009). For example, individuals with high between-sex degree (a measure describing how many individuals of the opposite sex a focal individual is interacting with) during, or after, a breeding season might show higher divorce rates as they sample more potential partners. On the other hand, individuals with high between-sex degree prior to a breeding season might show a lower probability of later divorce as they have had the opportunity to sample a larger number of members of the opposite sex, and thus choose the best possible partner for themselves amongst them. Moreover, the members of a breeding pair can be viewed as a (very small) social network. The dynamics of this two-member network over the non-breeding period can give valuable insights into the processes of pair formation and dissolution.

Study system and data collection

Great and blue tits

Great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) are small, relatively short-lived, cavity-nesting passerines. They are resident in the UK and spend winter in mixed species flocks composed of variable numbers of individuals (Gosler 1993). Recorded divorce rates are highly variable in both great tits (from 0% to 51% of surviving pairs), and blue tits (from 8% to 85%). The majority of studies on divorce in blue and great tits have looked at reproductive causes and consequences of divorce. It seems that regarding breeding performance prior to divorce, pairs that will later divorce do either less well or as well as faithful pairs, but never better (e.g. Perrins and McCleery 1985, Dhondt et al. 1996, Szulkin and Sheldon 2008). However, when it comes to breeding success after divorce, the general conclusions are less straightforward, with some studies reporting increase in breeding success after divorce (Dhondt et al. 1996), some decrease (Perrins and McCleery 1985), and some no change (Pampus et al. 2005). Winter social organisation (whether pairs spend winter in the same or different flocks) and residency have been rarely considered as factors influencing divorce probability. Divorce was found to happen more often in great tit pairs that belonged to different flocks prior to pair formation (Saitou 2002), and in populations with lower rates of winter residency of breeders (Dhondt et al. 1996). Although the great tit is one of the most commonly studied bird species, knowledge about the process of pair formation and dissolution, winter social behaviour and its influence on pairing outcomes is still very sparse.

The majority of the data used in this thesis come from wild populations of great tits at two woodlands near Oxford (Wytham Woods and Bagley Wood); some of the data come from blue tits in Wytham Woods. Wytham Woods (51° 46’ N, 1° 19’ W, Fig 1) is a mixed deciduous woodland of c. 385ha, with a canopy composed primarily of oak (*Quercus robur*), ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*) and beech (*Fagus sylvatica*). Bagley Wood (51° 42’ N, 1° 15’ W) is c.250ha woodland, consisting of a matrix of mixed pine plantations, and deciduous plots dominated by mature oak trees. The great tit population in Wytham has been studied since 1947, and since the early 1960s using standard protocols (Perrins 1965, Perrins 1979, Gosler 1993). Since the standardized protocol has been used, more than 11 500 breeding attempts of 12 000 individuals in Wytham great tits have been recorded. The blue tit population study began, in its current form, in 2001, and has resulted in the collection of more than 3300 breeding attempts of 3400 individuals. This provides a great wealth of background information on basic ecological processes and the determinants of fitness within populations, as well as (of most importance to this study) a large data set to conduct more powerful analysis. Study of the populations in Bagley Wood started, in its present form, in 2007. In both woods nest boxes are provided and more that 99% of great tit pairs and more than 90% of blue tit pairs are estimated to breed in them (Perrins 1979).

Together with data on breeding attempts, I used data on the winter social behaviour of great tits. These data have been collected in some detail since 2007 in Wytham Woods (see Fig 1), using radio-frequency identification (RFID) technology (Garroway et al. 2014). Birds marked with passive integrated transporters (PIT-tags) were recorded when they landed on feeders equipped with antennae (Francis Instruments Ltd, Cambridge). Each feeder was filled with sunflower seeds, had two food-access holes, and one antennae placed on each of these holes. Sunflower seeds were chosen as a food because individuals generally picked up a seed and processed it in a nearby tree, minimising queuing (and thus the competition) on a feeder. Loggers scanned for PIT tags every 1/16th of a second from pre-dawn until after dusk. Records of the individual’s unique PIT-tag identity (which is cross-referenced to its unique ring number), the time and date of the visit were stored into a log file. These files form a data stream that contains the information on the time and location of individuals visits, later used to infer group membership (Psorakis et al. 2012). Birds received PIT-tags when they were ringed for the first time (either as breeders, hatchlings, or during winter catching). It has been estimated that approximately 80% of all the birds ever available for PIT-tagging were indeed tagged (Matechou et al. in press). During the winters of 2007/08, 2008/09 and 2009/10 data were collected between August and March at 67 loggers. At any time, 16 of these loggers were automatically opened (and thus available for birds to feed). Every four days open loggers were rotated around the 67 locations following a structured randomised design, so that each of 8 approximately equally-sized sections of the woods always contained two active loggers. In the 2011/12 and 2012/13 winters there were 65 feeders which were simultaneously opened once a week, for two subsequent days, between December and March. Given that each logger was open only every several days, the possibility that flocks would get attracted to the constant food sources was minimised, and we assume that data gathered at feeders represent a ‘snapshot’ of the social composition at the time of feeding. Feeders were also maintained filled with food at all times, ensuring no patch depletion.

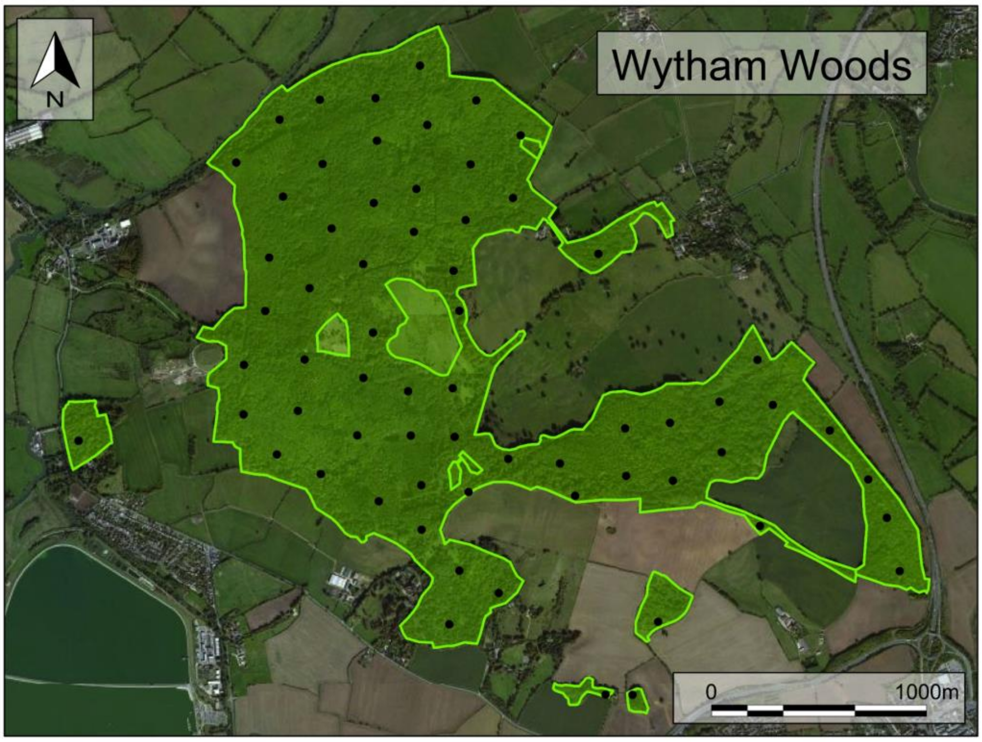

Figure 1. Map of Wytham Woods, United Kingdom (51° 46’ N, 1° 19’ W). Black dots mark the location of feeders equipped with PIT-tag detecting antennae in the 2011/2012 and 2012/2013 winters. The distance between the feeding stations was approximately 250m.

Abbotsbury mute swans

Mute swans (*Cygnus olor*) are large, long-lived birds. This species is sedentary in the UK, with the majority (i.e. ~ 97%) of birds staying in their natal area (Birkhead and Perrins 1986). Although mute swans are a paragon of monogamy in birds, surprisingly little is known on their fidelity (except that the fidelity rates are high). The majority of birds first breed when they are three or four years old (Perrins et al. 1994, Coleman et al. 2001), and have only one partner in their lifetime (around 84% of breeders, Rees et al. 1996, around 50% of breeders, Coleman et al. 2001). However, up to five mates have been recorded (Perrins and McCleery 1997). Pair duration varies between 1 and 16 years (mean = 3.3, sd = 3.1, n = 354, Rees et al. 1996), and breeding success seems to increase up to 5 years of pair duration, after which it levels off (Rees et al. 1996). Rates of fidelity are assessed to be high (around 90% of birds that survive breed with the same partner as in the last breeding season (Perrins and McCleery 1997). Divorce rates are reported to be low – in pairs where both partners survived between the two breeding season 4% (Rees et al. 1996), 6% (Perrins and McCleery 1997), and 20% (Coleman et al. 2001) divorced. It has been estimated that it takes 1.5 years (sd = 0.8, range 1- 4) to resume breeding after changing a mate (Rees et al. 1996). Birds that have replaced mates were also found to produce fewer cygnets compared to birds of faithful pairs, but only when the replacement mate was a non-experienced breeder (Rees et al. 1996). However, when the replacement mate was an experienced breeder, the difference disappeared. Moreover, the effects of the number of mates on the lifetime breeding success were not detected (Rees et al. 1996).

The data for mute swans I use in this thesis come from a long–term monitored colony that breeds at the Abbotsbury swannery (Dorset, 50 °39’ N, 2 ° 36’ W). Intensive monitoring of the colony started in 1977, with the number of breeding pairs fluctuating between 18 and 130. A detailed description of the study site is provided in Perrins and Oglivie (1981) and Perrins et al. (1994). Together with the standard BTO metal ring, birds are also ringed with an engraved plastic (darvic) ring. This makes it possible for birds to be identified in the field, without catching. The majority of breeders (80-90%) are ringed as cygnets (Perrins et al. 1994). Thus, the exact age for most of the birds is known (including immigrants that are captured in their first or second year). The monitoring of the breeding pairs in the colony resulted in approximately 3600 breeding attempts by 1600 breeders (males and females) being recorded.

Thesis aims and overview

The main aims of this thesis are to increase our understanding of causes, processes and consequences of mate fidelity and divorce in monogamous birds. Specifically, my aims are to (1) evaluate the generality of the relationship between divorce and breeding success in monogamous birds, and relate this to life-history traits that might shape reproductive costs and benefits of divorce; (2) study survival as a possible important fitness consequence of different mating outcomes, using different species (blue tits, great tits, and mute swans); (3) develop a method to asses accurate and unbiased rates of fidelity, which can be easily extended to test hypotheses on fidelity and to be applied not only to breeding relationships but to any kind of time varying association between two individuals; (4) explore the importance of the social environment (described through the social network position of an individual) in which a pair forms and the length of this period to the later breeding success and divorce probability of a pair. To address my aims, I use three novel approaches: (i) recently refined methods for phylogenetic meta-analysis, applied across a large number of studies on divorce in monogamous birds; (ii) multievent mark-recapture modelling (Pradel 2005, Pradel et al. 2008); and (iii) social network analysis (Krause et al. 2007) applied to the long-term breeding data and winter feeding data of the two populations of great and blue tits.

This thesis consists of six data chapters.

In **Chapter 2** I set to establish whether between-season divorce is adaptive or not in terms of breeding success across monogamous bird species. Although the main current approach of studying adaptiveness of divorce in monogamous birds is through correlating breeding success to the occurrence of divorce, there is no consensus among empirical studies on this central question. I thus conduct a robust phylogenetic meta-analysis on 84 studies across 64 monogamous bird species exploring the directionality (and strength) of the relationship between breeding success, and the occurrence of divorce. In addition, I explore biological and methodological reasons for the heterogeneity in the results of previous studies.

In **Chapter 3** I overcome current problems faced by studies that try to understand what factors influence the individual-, population-, and species-specific rates of fidelity. These studies relate attributes of interest to the estimated fidelity or divorce rates of individuals, species or populations. However, due to methodological problems in data collection, uncertainly in pair status assessment, and the heterogeneity of recapture rates of marked individuals, current methods for assessing pair fidelity are imprecise and potentially biased. Even more, survival, as an important component of fitness, is rarely addressed as a possible consequence of mating outcomes. Together, these might lead to faulty conclusions about causes, consequences and correlates of pair fidelity. Thus, I develop a novel probabilistic multievent capture-mark-recapture framework that provides joint estimates of survival and fidelity while explicitly accounting for imperfect detection, capture heterogeneity, and uncertainty in pair-status. I apply the approach to 30 years of breeding data from the population of great tits breeding in Wytham Woods, Oxford.

In **Chapter 4** I explore the generality of the findings from Chapter 3 by addressing the influence that current pair status has on survival and future pairing outcomes in two different populations of great tits, and in a population of blue tits. In addition, I explore which components of survival and which correlates of fidelity are shared between species or populations, and which are population- and species-specific. I use the finding of the analyses to discuss the importance of life-history, fine-scale, and large-scale environmental influences on fidelity rates, and the correlation between fidelity and survival.

While in Chapters 3 and 4 I concentrated on two short-lived species, with high annual mortality rates, in **Chapter 5** I address the potential survival and breeding benefits of fidelity to a partner in a long-lived species, with a generally high survival rate. I use 34 years of data on breeding pairs of mute swans. In addition, exploring the heterogeneity of fidelity rates and fidelity-fitness correlates among individuals within the same population is important for understanding population and species level patterns of fidelity. Thus, I also look at how several individual traits (age, stage of breeding lifetime, and immigration status) influence the probability of staying faithful and the fitness correlates of fidelity.

In **Chapter 6** I further explore individual-specific fidelity and divorce rates by focussing on the immediate social environment individuals are exposed to during initial mate choice. Initial mate choice, and later mating decisions (i.e. infidelity and divorce), should be affected by the constraints individuals face, including the number and availability of potential partners. Studies have so far addressed the influence of the social environment only indirectly (i.e. using population-level demographic factors), and only after a pair has already bred. I address the importance of the social environment in which a pair of great tits has formed to later mating outcomes (i.e. fidelity and divorce). I do this by using detailed data on the winter social networks of tagged birds which allow me to describe the number of associates of the opposite sex, the rank of the future partner amongst these, and association strength between the members of the future breeding pair.

In **Chapter 7** I address direct and indirect importance of the length of the initial pairing period to breeding success and the probability of divorce in great tit pairs. While the ‘mate familiarity effect’ has been proposed as one of the main factors contributing to increase in breeding success in subsequent breeding attempts of a pair, the importance of association with a partner prior to the first breeding of a pair remained largely unexplored. I use detailed data on the associations of individually marked great tits in Wytham Woods over 5 winters to detect the time when a pair started to associate. Specifically, I explore which components of breeding success benefit from the longer period of pre-breeding association directly, and which indirectly (i.e. mediated through previous components). Similar, I look at indirect (i.e. mediated through breeding success) and direct effects of the initial pairing period on the later divorce probability of a pair.

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CHAPTER 2

Trading up: the fitness consequences of divorce in monogamous birds

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Trading up: the fitness consequences of divorce in monogamous birds

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ABSTRACT

Social and genetic mating systems play an important role in natural and sexual selection, as well as in the dynamics of populations. In socially monogamous species different genetic mating patterns appear when individuals mate outside the breeding pair within a breeding season (extra-pair mating) or when they change partners between two breeding seasons (widowing or divorce). Divorce can be defined as having occurred when two previously paired individuals are alive during the next breeding season and at least one of them has re-mated with a new partner. In socially monogamous birds divorce is widespread, but it is not clear whether it is a behavioural adaptation to improve the quality of a mating decision or whether, alternatively, it results as a non-selected consequence of other processes: existing studies suggest a heterogeneous set of results with respect to this central question. This heterogeneity could result from a number of factors, ranging from the methodological approaches used, to population- or species-specific characters. In this review we use phylogenetic meta-analyses to assess the evidence that divorce is adaptive (in terms of breeding success) across 64 species of socially monogamous birds. Second, we explore biological and methodological reasons for the heterogeneity in the results of previous studies. Results of our analyses supported the hypothesis that divorce is, in general, an adaptive behavioural strategy as: (1) divorce is triggered by relatively low breeding success; (2) there is a positive change in breeding success as a result of divorce. More specifically, while controlling for methodological moderators, we show that: (*i*) earlier stages of breeding are better predictors of divorce than later stages ($r = 0.231$; 95% CI: 0.061–0.391 for clutch size; similar for laying date); (*ii*) females benefited from divorce more than males in terms of increasing breeding success between successive breeding attempts, with different stages of the breeding cycle improving at different rates (e.g. $r = 0.637$; 95% CI: 0.328–0.817 for brood-level measures). We show that the effect size was dependent on the methodological approach used across studies and argue that research on the adaptive nature of divorce should be cautious when designing the study and interpreting the results. Altogether, by providing strong evidence that divorce is an adaptive strategy across monogamous birds, the results of our analysis provide a firm ground for further exploration of external covariates of divorce (e.g. demographic factors) and the mechanisms underlying the differences in the effect sizes of the proximal fitness causes and consequences of divorce.

Key words: divorce, birds, breeding success, meta-analysis, life history, fitness, monogamy, mating, adaptiveness, sexual selection.

CONTENTS

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I. INTRODUCTION

The evolution and emergence of different mating systems has been a topic of considerable interest both within the scientific community, and also in the non-scientific community (Quinlan & Quinlan, 2007; Kappeler, 2013). Mating systems were first classified based on the observed patterns of pairings between sexes and their share in the care for offspring. However, after techniques to determine genetic parentage were developed, it has been suggested that mating systems should be classified at two levels: as social mating systems, and as genetic mating systems, the latter usually being defined using the patterns of extra-pair matings (Bennett & Owens, 2002; Griffith, Owens & Thuman, 2002). These genetic mating systems are especially interesting to study in birds, where more than 85% of species are socially monogamous but only 25% of socially monogamous birds are genetically monogamous (Bennett & Owens, 2002; Griffith *et al.*, 2002). Both extra-pair mating (which happens within a breeding season), and partner change (which usually happens between breeding seasons, but can also happen within a breeding season) will reflect short-term (i.e. within season) and long-term (i.e. over an individual's lifespan) genetic mating systems. The level of maintenance of pair bonds will depend on levels of widowing (i.e. one partner dies) and levels of divorce (i.e. both partners are alive, and at least one of them has re-mated with a new partner, Black, 1996; however, we note that, while divorce has been defined by all of the empirical studies that we review as occurring when re-mating with a new partner occurs for at least one member of a surviving pair, broader definitions are conceivable. For example, in resident species, it might be possible to define divorce as having occurred when one member of a pair moves from a formerly jointly defended territory, or when a marked change in social affiliation occurs). Understanding the emergence of social and genetic mating systems of species and populations, and mating strategies that individuals adopt, can help understanding of natural and sexual selection (Reichard & Boesch, 2003; Shuster & Wade, 2003).

Because biparental care (and thus social monogamy) is essential in the majority of monogamous bird species (Bennett & Owens, 2002), extra-pair copulations and divorce have frequently been suggested to represent a way to correct for suboptimal social partnerships, which may result from different types of constraints on the initial mate choice (Johnston & Ryder, 1987; Moller, 1992; Sullivan, 1994; Choudhury, 1995; Botero & Rubenstein, 2012), or/and to secure genetically more diverse offspring (see references in Arnqvist & Kirkpatrick, 2005). Divorce has been recorded in 92% of socially monogamous birds (Jeschke & Kokko, 2008), with divorce rates being highly variable both among species and within species (Black, 1996). Two main attributes of divorce make it particularly interesting to study. First, divorce can potentially affect fitness by influencing breeding success and survival. Second, divorce could be seen as a mate-choice mechanism in which prior breeding performance may be used as a cue to determine the choice to stay with, or to leave the partner (Choudhury, 1995). If divorce influences fitness or pairing decisions, we can also expect it to shape population productivity and dynamics (Sugg *et al.*, 1996; Berec & Boukal, 2004; Maxin & Berec, 2010), and the genetic structure of populations (Sugg *et al.*, 1996; Cézilly & Zayan, 2000).

Two main groups of hypotheses explain divorce either as an adaptive strategy of at least one member of a pair to increase breeding success, or as a non-adaptive event, either happening by chance, or as a byproduct of another strategy (see review by Choudhury, 1995). If divorce represents a form of adaptive mate choice, it should be triggered either by low breeding success (Dubois & Cézilly, 2002) or by the potential to improve breeding success with a new partner (Choudhury, 1995; Black, 1996), or both. That is, divorce could be seen as a response to poor conditions, or to the prospect of better conditions; these need not be independent. By contrast, if divorce happens by chance, by usurpation, or as a non-selected effect of some other process, it should not correlate with breeding success in the season before, and should lead either to a decrease or to no change in overall breeding success. Empirical studies relating breeding success to the occurrence of divorce have not reached a consensus on whether divorce can be regarded as an adaptive mating strategy. The results of individual studies vary greatly, ranging from those finding a negative correlation and no correlation (e.g. Handel & Gill, 2000; Pampus, Schmidt & Wiltschko, 2005; Wysocki, 2006) to those finding positive effects (e.g. Dhondt & Adriaensen, 1994; Moody *et al.*, 2005).

Given the lack of a clear pattern in the results of the studies on the adaptiveness of divorce two main questions emerge: (1) is there any clear overall relationship between breeding success and divorce, and if there is, how strong is this and does it support divorce being an adaptive strategy? (2) What causes variation in the relationships found in the different studies? Meta-analysis is the appropriate way to approach these questions as it is designed to enable assessment of general conclusions from individual studies and multiple correlations (Cadotte, Mehrkens & Menge, 2012; Nakagawa & Poulin, 2012). By taking into account the magnitude of effects (i.e. effect sizes), sampling errors and sample sizes, all of which influence statistical power, meta-analytical techniques can detect significant effects even when individual studies (or effect sizes) are non-significant (Cadotte *et al.*, 2012; Nakagawa & Poulin, 2012). Moreover, meta-analysis offers a range of methods to detect publication bias (Table 1 in Jennions, Lortie & Rosenberg, 2013) and to account for other types of possible biases (e.g. data quality). Finally, meta-analysis is a powerful tool to test hypotheses about the biological mechanisms causing variation in effect sizes. Recently developed mixed-effect meta-analysis and phylogenetic meta-analysis (Hadfield & Nakagawa, 2010) allow for data with multiple correlated structures (e.g. multiple effect sizes per study or species) and phylogenetic relatedness to be analysed in one coherent statistical framework.

In this study, we apply phylogenetic mixed-effect meta-analyses to a data set relating to the fitness causes and correlates of divorce in wild bird populations, comprising 81 studies of 64 socially monogamous bird species, with 437 individual effect size estimates. We sought to use these data to: (*i*) test whether it is plausible to consider divorce as an adaptive mating strategy; (*ii*) explore the costs and benefits of divorce in relation to sex, stage of reproductive cycle, and species-specific traits; (*iii*) test the validity of common methodological approaches used in studies of the relationship between divorce and breeding success, and provide guidelines for conducting field studies and (*iv*) test for publication bias. There has been only one previous meta-analysis on divorce and breeding success in birds (Dubois & Cézilly, 2002). That study included 38 studies on 35 socially monogamous bird species and found a small but significant effect of the average weighted effect size of previous breeding success (defined as fledging at least one chick) on the probability to divorce ($r = 0.111$, $P < 0.0001$). Our meta-analyses build upon this previous study by: (*i*) increasing the sample size; (*ii*) including studies reporting not only the effect of previous breeding success on divorce probability, but also reporting the change of breeding success and breeding success after divorce; (*iii*) including measures of breeding success other than fledging success; (*iv*) including effect sizes estimated from continuous measures of success, not only success categorized as a binomial character; and (*iv*) using new statistical methods that offer more flexibility to include non-independent effect sizes, moderator variables and phylogenetic structure in the same analysis.

Table 1. Categories and subcategories of the stage of the breeding cycle when breeding success was measured used to study their influence on the effect size of the relation between breeding success and divorce in birds

Main category	First subcategory	Second subcategory
Skipped breeding	Skipped breeding	Skipped breeding
Timing of breeding	Timing of breeding	Timing of breeding
Clutch size	Clutch size	Clutch size
Brood	Hatching success	For all pairs laying a clutch
		For pairs that hatched young
	N of hatched young	For all pairs laying a clutch
		For pairs that hatched young
Fledging	Fledging success	For all pairs laying a clutch
		For pairs that hatched young
		For pairs that fledged young
	N of fledglings	For all pairs laying a clutch
		For pairs that hatched young
		For pairs that fledged young

II. HYPOTHESES TESTED

First, we test whether there is overall evidence for divorce being adaptive across bird species. To do this we conduct one global meta-analysis on the full set of data encompassing all the effect sizes, where breeding success is either measured before divorce (i.e. at time $t-1$), after divorce (i.e. at time t), or as a change of breeding success (i.e. difference between success at t and $t-1$); we also break this down and conduct three separate analyses for each of these three temporal contrasts. If divorce is adaptive we expect divorced individuals or pairs to show lower breeding success prior to divorce (i.e. low breeding success triggers divorce, Fig. 1A), and to improve in breeding success more between attempts (Fig. 1B) than individuals or pairs that stay faithful or are widowed. However, breeding success after divorce might still be lower for divorced birds than for other birds, because of the possibility that they would have done even worse had they stayed with their former partners (Fig. 1A), and because of initial costs of partner change. Thus, divorced birds can have lower breeding success compared to faithful birds even if divorce is an adaptive strategy.

Next, we test how several life-history variables (stage of breeding cycle, sex, longevity, coloniality, site fidelity, extra-pair brood rates, and divorce rates) influence the relationship between divorce and breeding success; some of these effects are study-specific; others are species-specific. The stage of the breeding cycle at which breeding success was measured might influence the effect size because: (*i*) effects of environmental stochasticity (e.g. food abundance; Ponchon *et al.*, 2014) on breeding success accumulate over the different breeding stages, and this could be expected to reduce the strength of correlation between divorce and breeding success at the later stages of the breeding cycle. In addition, parents are thought to be better able to adjust to fluctuating environments at earlier stages (see Lindström, 1999); (*ii*) familiarity with a partner (e.g. synchronisation of parental duties) increases with the stage of breeding cycle, increasing the benefits of staying with the same partner to the next season, and consequently reducing the response to low breeding success at later stages; (*iii*) different components of breeding success might convey different types of information (e.g. partner quality) upon which a decision to divorce is based, as well as offer different scopes for improvement. For example, low hatching success is a common form of inbreeding depression (van Noordwijk & Scharloo, 1981; Bensch, Hasselquist & Vonschantz, 1994; Kempenaers *et al.*, 1996) and might serve as a cue to avoid mating with genetically similar individuals. Moreover, scope for improvement in a certain component of breeding success might be different for females and males. For example, clutch size, as a plastic trait, is thought to reflect female condition (Hogstedt, 1980; Slagsvold & Lifjeld, 1990; Bety, Gauthier & Giroux, 2003) and males might divorce females to improve the clutch size produced by their partner. Accordingly, we test if the effect size is higher at earlier stages of reproduction, and whether the effect size differs between females and males.

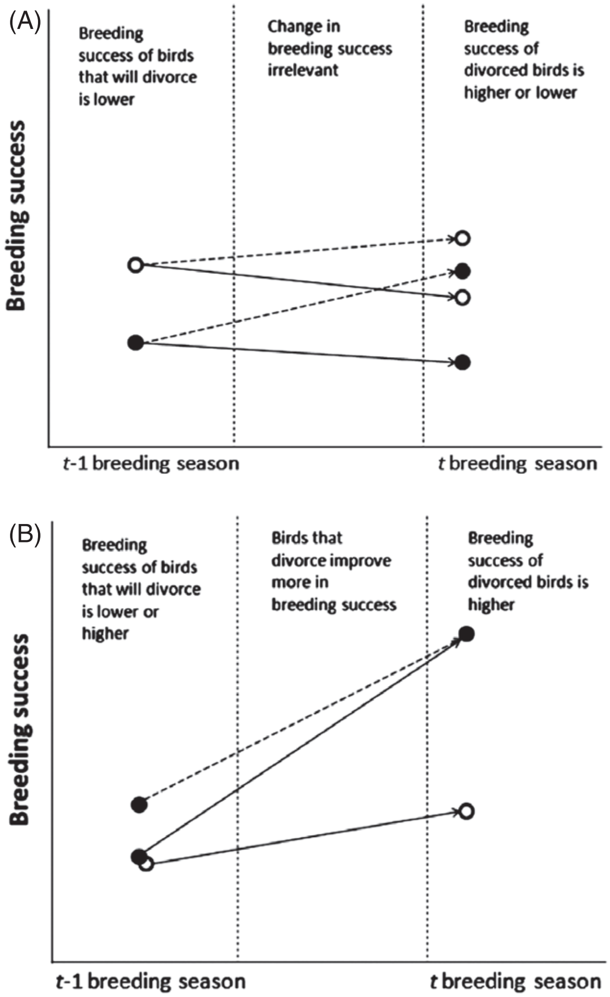

Fig. 1. An illustrative example of the main scenarios on how breeding success [before divorce ($t-1$), after divorce (t), change in breeding success between the two seasons] of divorced birds (black circles) is expected to relate to breeding success of a reference pairing class (usually faithful birds, empty circles). (A) If divorce is an adaptive strategy divorced birds have initially lower breeding success than the birds of a reference pairing class. Because the change in breeding success can go in any direction, the breeding success divorced birds achieve in the season after divorce can be both higher and lower than the breeding success of the reference pairing class. (B) Divorced birds have same initial breeding success (or even higher success, dashed arrow) compared to the reference pairing class but they always improve more in the next breeding season. Consequently, they also have higher breeding success in the season after divorce compared to a reference pairing class.

Several life-history traits have been suggested to affect the correlation between breeding success and divorce (Rowley, 1983; Jouventin & Bried, 2001; Bried, Pontier & Jouventin, 2003). This can happen through the influence of life history on the possible fitness gains of divorce (for example, maximal clutch size), and on the additional costs to divorce (e.g. costs of obtaining a new partner). When life history causes any additional costs, we expect to see an increase in the effect size because additional costs demand a higher pay-off. Here we test the following hypotheses: (1) by divorcing, long-lived species do not improve their breeding success in the season immediately following divorce (no study in our meta-analyses reported measures of breeding success in later breeding seasons) because the benefits of divorce do not necessarily have to outweigh the costs in the first season after divorce, as long as it improves later (i.e. in subsequent seasons; Williams, 1966; Stearns, 1992); (2) for colonial species the effect sizes are smaller (if positive) than for non-colonial species, because colonial species have easier access to potential future mates for which they might divorce their current partner (Dubois, Cézilly & Pagel, 1998); (3) the effect sizes for species forming part-time partnerships such as many migratory species will be close to zero. The costs of waiting for the former mate, who might even not be alive, could outweigh the benefits of fidelity and the costs of finding a new partner (Rowley, 1983; Bried & Jouventin, 2002; Ludwig & Becker, 2006). Consequently, we expect selection for divorce to be very weak, and less likely to evolve as an adaptive strategy for those species. A related problem is that of site fidelity. Because site and mate fidelity are often correlated (high-quality males tend to occupy high-quality territories; e.g. Handel & Gill, 2000; Cézilly, Dubois & Pagel, 2000*a*), we explore whether the effect size of the relationship between breeding success and divorce is influenced by species site fidelity. Following similar reasoning about the release or addition of costs according to life-history traits, we tested whether divorce and extra-pair brood rates of a species (or population, see Section III) influence the effect size. There are two possible scenarios as to how effect size should relate to divorce rates. The first possibility is that increased divorce rates in a population reflect low costs of divorce (or low benefits of fidelity), in which case we expect lower effect sizes with increased divorce rates. On the other hand, high divorce rates might reflect high benefits of divorce, in which case we expect an increase in the effect size with increased divorce rates.

As well as testing biological hypotheses, we aim to provide guidelines on how to conduct studies on the fitness correlates of divorce. We consider how two very common approaches that studies on divorce have taken can influence effect sizes (and consequently, conclusions about the adaptiveness of divorce). The first relates to the dichotomisation of otherwise non-binary measures of breeding success (for example if a study considers fledging ≥1 offspring as success, and fledging none as a failure, instead of taking into account the exact number of fledglings). The second is the use of a reference pairing class to which breeding success of divorced birds is compared (e.g. population mean, widowed or faithful pairs/individuals). Finally, we test for publication bias in our data set, using a range of methods, as reviewed by Nakagawa & Santos (2012).

III. METHODS

(1) Data collection

To locate studies reporting correlations between breeding success and divorce, we searched the *Web of Science* research platform for literature published before 1 January 2013. We used the following search terms: *mate change, partner change, divorce, mate switching, mate retention, remating, widowing, faithfulness, fidelity, pair fidelity, pair faithfulness, partner fidelity, partner faithfulness, pair dissolution, pair bond*, in combination with search terms describing breeding success: *breeding success, breeding output, reproductive success, reproductive output*, and three general terms that are possible to relate to breeding success: *causes, consequences, correlates*. We also performed forward and backward literature searches of studies obtained by the initial search. Only studies providing all information needed to calculate at least one effect size (i.e. reporting test statistics together with the sample size and direction of the effect, and/or the raw data, see online Appendix S1, Table S1) were included in the analyses. When it was not possible to calculate the effect size (if the information provided was insufficient or ambiguous, e.g. sample sizes reported in the text did not correspond to those presented in tables or figures) we contacted the author. If we did not receive any further information we excluded the effect sizes for which information was lacking. If two, or more, effect sizes were reported for nested categories (e.g. for all females and then separately for juvenile and adult females) we kept only the most general category, except when the effect sizes were reported for males and females separately. Our final data set comprised 81 studies (published between 1966 and 2013) on 64 species (Fig. 2), with 437 effect sizes.

For each effect size we coded three methodological moderators, and 10 biological variables that we expected to influence the effect size. The methodological moderators were: (*i*) data quality, reflecting personal assessment of how much the data can be trusted, with three levels (details on the procedure we applied to assess data quality are provided in the online Appendix S1); (*ii*) dichotomisation with three categories: 'binary', 'non-binary but dichotomised', and 'non-binary and non-dichotomised'. Category 'binary' includes species producing only one egg where there are only two possible outcomes and skipped breeding (success or not). When a species produces more than one egg, then breeding success can be expressed as either exact number of eggs/hatchlings/fledglings (category 'non-binary and non-dichotomised'), or reduced to a dichotomised measure (producing at least one hatchling/fledgling, or not); (*iii*) reference pairing class to which breeding success of divorced birds was contrasted: faithful, widowed, population mean, or comparison of breeding success at $t-1$ and at t for the divorcing individual itself.

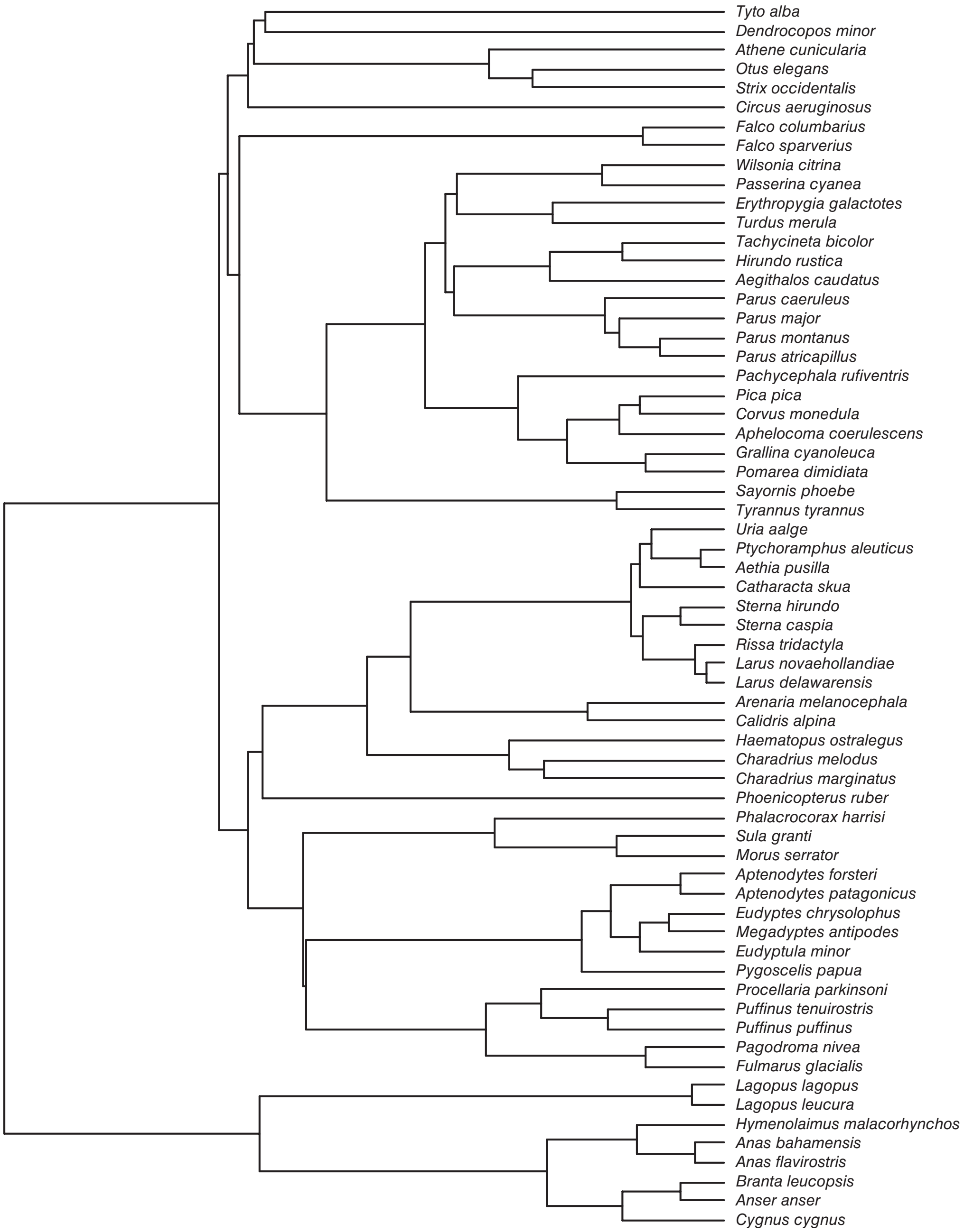

Fig. 2. An example of one of the 100 phylogenetic trees of species included in the overall meta-analysis on the correlation between breeding success and between-season divorce.

The biological moderators were: (*iv*) whether breeding success was measured for individuals, pairs, males, or females; (*v*) stage of breeding cycle at which breeding success was measured, categorised at different levels (main categorisation and two sub-categorisations, Table 1), with main categories being skipped breeding (a bird is alive and present at the breeding ground, but does not breed), timing (this is laying date for all except two studies that reported hatch date), clutch size, brood (brood-level measures), and fledging (measures at the level of fledgling production); (*vi*) divorce rate of the species (mainly as reported in Jeschke & Kokko, 2008) measured as the percentage of surviving pairs that divorce; (*vii*) species-specific longevity; value was obtained either directly, or calculated from survival rates using Seber's formula (Seber, 1973): $0.5 + 1/(1 - \text{survival rate})$; (*viii*) coloniality with three categories: non colonial, forming loose colonies, colonial; (*ix*) continuity of partnership with two categories: continuous partnerships and part-time partnership, reflecting whether pair members stay in spatial/social contact between two breeding seasons; (*x*) site fidelity with three categories: weak, medium, and strong; (*xi*) extra-pair brood rates (from Botero & Rubenstein, 2012) measured as percentage of broods containing extra-pair offspring; (*xii*) relative clutch size; (*xiii*) developmental mode (mainly taken from Sibly *et al.*, 2012) with two categories: atricial and precocial.

We obtained values for species longevity, coloniality, continuity of partnership, and relative clutch size mainly from Botero & Rubenstein (2012), Jeschke & Kokko (2008), del Hoyo, Elliott & Sargatal (1992, 1994), del Hoyo, Elliott & Sagital (1999) and del Hoyo, Elliott & Christie (2004, 2009). The exact source of information for each species is given in the online supporting information (see online Appendix S1, Table S2). Data on the continuity of partnership, site fidelity, extra-pair brood rates and divorce rates were available for a subset of species.

We calculated phylogenetic relationships among species using the Global phylogeny of birds web tool (Jetz *et al.*, 2012), which returned a set of 100 trees (as a minimum of trees that can be obtained). As Jetz *et al.* (2012) advise that 'any further analysis should only be conducted with a larger sample of trees', whenever our model included species as a phylogeny, we reran it with all 100 trees. In the results we present the outcomes for one randomly selected tree. The histograms of the effect sizes obtained by the repeated (100) runs of the best model for each meta-analysis are provided in Appendix S2 (Figs S1–S3) and show that the mean effect sizes of all 100 trees fall well within the credible intervals of the one randomly selected tree for which we present the results in the main text.

(2) Calculating effect sizes

For each data point, we first calculated the effect size as a Pearson's correlation coefficient, r, using either the 'raw' values reported in the paper (mean and error measure of breeding success of contrasted pairing classes, i.e. divorced, faithful, widowed; or contingency table, i.e. number of successes/failures in a certain pairing class given breeding success measure) or the corresponding test statistics (together with sample size and the direction of the effect). The exact procedures and formulae we used to calculate r are given in Appendix S2. After we calculated r, we transformed it into Fisher's Z (Z_r) using the formula provided by Nakagawa & Cuthill (2007). We used Z_r (which has a normal distribution) as the response variable in the meta-analysis, which was then back-transformed into r for the presentation of results.

We assigned the biological direction of the effect size as positive if it implied that divorce is an adaptive strategy and negative if it implied that divorce is not adaptive. When breeding success achieved in the season before divorce (we termed this $t-1$) was compared between birds that would later divorce and the reference pairing class, we assigned a positive value to the effect size if the breeding success of divorced birds was lower than the breeding success of the reference pairing class, and negative if it was higher. When breeding success was compared between divorced birds and the reference pairing class in the season after divorce (we term this t) or expressed as a change in breeding success (between $t-1$ and t), then we assigned a positive direction to the effect size when divorced birds had higher breeding success in the season after divorce/greater positive change in breeding success between the two seasons than the reference pairing class (see Fig. 1).

(3) Meta-analytical and meta-regression procedures

We conducted four separate sets of meta-analyses using the 'MCMCglmm' package in R (Hadfield, 2010). We used the 'APE' package (Paradis, Claude & Strimmer, 2004) to implement phylogenetic trees into MCMCglmm. We based model selection on the deviance information criterion (DIC), which is a Bayesian analogue of Akaike information criterion (AIC, Spiegelhalter *et al.*, 2002). Because DIC relies on posterior distributions to approximate normality, we visually inspected the posterior distributions for non-normality. We considered a model that had the DIC value more than 4 units lower to be a better fit to the data than the competing model (or models). In addition, for each set of models, we also checked the significance of the fixed effects included in the models (using P-values provided in the MCMCglmm as pMCMC). The first meta-analysis encompassed all of the effect sizes (breeding success was measured before divorce, after divorce, or as a change in breeding success) to find the overall effect size (r_{overall}) using random-effect modelling (as described below, **first step**). As expected, inclusion of the time when breeding success was measured into the fixed part of the model considerably improved the fit ($\Delta\text{DIC} = -115.95$), with effect sizes being marginally (i.e. 95%CI overlap zero) positive for the correlation between breeding success at $t-1$ and occurrence of divorce, and change in breeding success and divorce, and negative for the correlation between divorce and breeding success at t (see online Appendix S2, Fig. S4). This finding supported our decision to conduct three separate meta-analyses on the subsets of data given the time when breeding success was measured: (*i*) breeding success was measured before divorce, at $t-1$ ('before' meta-analysis, r_{before}); (*ii*) breeding success was expressed as a change in success between the two seasons, t and $t-1$ ('change' meta-analysis, r_{change}); (*iii*) breeding success was measured in the season straight after divorce, at t ('after' meta-analysis, r_{after}). Corresponding sample sizes (number of species, populations, and effect sizes are given in Table 2). For each meta-analysis on the subset of data we applied the same modelling approach, as described below.

In the **first step** of each analysis, we estimated the overall effect size using mixed-effect models with 'species'

Table 2. Number of species, populations and effect sizes included in three different meta-analyses for the correlation between divorce and breeding success

Data set	Number of species	Number of populations	Number of effect sizes
Before	50	64	179
Change	23	33	126
After	32	35	128

and 'population' (i.e. when there are two or more independent samples of individuals within the study and effect sizes for these are reported separately) as random effects. This allowed us to account for multiple effect sizes per species and population, and to explore how much variation in the data can be attributed to these levels. As a lack of independence in the data set can be caused by phylogenetic relationships among species, we also incorporated species as the phylogenetic covariance structure (phylogenetic meta-analysis; Hadfield & Nakagawa, 2010). We constructed a separate tree, with relevant species, for each meta-analysis (see online Appendix S2, Figs S5–S7). We took the simple random-effect model in which we treated data as completely independent as the null model against which we compared the performance of four different models with hierarchical random-effect structure of population, species (without taking phylogeny into account), phylogenetic tree, and both population and phylogenetic tree (additive effect).

In the **second step**, we kept the best random-effect model obtained in the first step and included methodological moderators (data quality, dichotomisation, reference pairing class), both separately and in combination (additive effect), to the fixed part of the model. To explore further the possible interaction between dichotomisation of the breeding success and clutch size, we included clutch size and its interaction with the covariate coding for dichotomisation. In the **third step**, we explored the influence of possible biological variables (stage of breeding cycle breeding success was measured at, sex, longevity, coloniality, continuity of partnership, extra-pair broods rate, and divorce rate) by including the corresponding variable of interest to the fixed-effect part of the model selected in the first two steps (i.e. with random structure and methodological moderators). When exploring the influence of breeding success we also compared the performance of the models with breeding success categorised at the main level, and two nested subcategories (see Table 1). We did not test whether measuring breeding success before divorce for pairs, males or females influenced the effect size because we did not expect these effect sizes to differ (e.g. if the measure was reported for females, it would be the same as if it was reported for males, or for pairs). In addition, because the age of breeders can influence breeding success (e.g. Pyle, Sydeman & Hester, 2001; Schmaltz, Cézilly & Bechet, 2011), divorce probability (e.g. Pampus *et al.*, 2005; Llambias, Wrege & Winkler, 2008), and recapture probability (Tavecchia *et al.*, 2001), and thus influence the overall effect size of the relationship between breeding success and divorce, we tested if effect sizes of studies that controlled for age (16, 8 and 18 effect sizes in 'before', 'change', 'after' data sets) differed from the effect sizes of studies that did not control for age. Finally, because the need for parental care at different stages of the breeding cycle differs among species (Sibly *et al.*, 2012) we tested if type of developmental mode (altricial *versus* precocial) influenced the effect size by including it both as an additive and interactive covariate (with breeding success) in the best model. To check whether longevity, coloniality, and clutch size are correlated (Ricklefs, 1977; Dubois & Cézilly, 2002), we performed a correlation test between these three, and found that they indeed were correlated ($N = 64$, Pearson's correlation coefficients: longevity and coloniality = 0.29; longevity and clutch size = −0.50, coloniality and clutch size = −0.54, all P-values < 0.018). Thus, when testing for the influence of longevity and coloniality on the effect size, we tested the performance of the model with both included in the fixed-effect part, and controlling for clutch size, against the performance of the best model selected in the first two steps. When studying the influence of continuity of partnership, site fidelity, extra-pair brood levels, and divorce rates, we used subsets of data for which we had information on these variables, and tested the performance of the model with and without (i.e. simple random-effect model, except when modelling site fidelity where we also included other life-history traits) the corresponding variable of interest. For all three meta-analyses summary of the model structures with corresponding DIC values and effect sizes are given in Appendix S2 (Tables S4–S26). Each analysis was run for 5000000 iterations, burn-in of 500000, and thinning interval of 10.

(4) Additional meta-analysis on extended data set, including effect sizes for partner change

Conclusions about the adaptiveness of divorce can also be drawn by comparing the effect size of the correlation between breeding success and divorce with the effect sizes of the correlation between any type of partner change (i.e. breeding with a different partner to the one from the previous year, regardless of the previous year's partner being alive or dead). If divorce is an adaptive strategy, than we expect to find that r_{before}, r_{change} and r_{after} have larger negative values or smaller positive values for studies reporting partner change than for those reporting divorce as defined here. To test for the presence of this pattern, we conducted a meta-analysis on an extended data set that included studies (or additional effect sizes from the studies already included in the previous meta-analyses) reporting on the correlation between breeding success and partner change. This added 15 studies of 11 species (see online Appendix S2, Fig. S8, added species are marked with an asterisk), and 159 effect sizes to the data set used in the previous analyses. We compared the performance of three models: (1) the model with the random structure of population and phylogenetic tree; (2) the model with the random structure of population and phylogenetic tree, and fixed effect of the type of partner change ('divorce' or 'partner change'); (3) same as (2) but with timing when breeding success was measured: before divorce/partner change, after divorce/partner change, as a change in breeding success between two season, or as the overall success (i.e. success in both seasons is summed).

IV. RESULTS

The global meta-analysis, which included the effect sizes for all three temporal contrasts (i.e. breeding success measure obtained before divorce, as a change in breeding success, or after divorce), revealed that the overall effect size of the correlation between breeding success and divorce in monogamous birds was small and not significantly different from zero. The estimate of r_{overall} from the best random-effect model was 0.049 (95% CI: −0.009–0.102, see online Appendix S1, Table S1), with non-independence of data being predominantly caused by the effect of multiple measures on the same population (explaining 42.3% of the variance, see online Appendix S1, Table S1). However, this overall small effect size was not surprising because the correlation between breeding success after divorce and the occurrence of divorce might still be negative even if divorce was adaptive because divorcing individuals may still have improved their breeding situation compared to that pre-divorce. Hence, treating effect sizes of the three different temporal contrasts as being equally informative might lead to flawed conclusions about the adaptiveness of divorce. Thus, we performed separate sets of meta-analyses on each of the three temporal contrasts.

(1) Correlation between breeding success before divorce and divorce

The effect size r_{before} represents the correlation coefficient between breeding success in the season before divorce and the subsequent occurrence of divorce. A positive value of r_{before} means that birds that later divorced had lower breeding success compared to a reference pairing class. As expected under the hypotheses that divorce is adaptive (i.e. low breeding success triggers divorce) we found that the overall mean r_{before} was positive ($r_{\text{before}} = 0.108$; 95% CI: 0.067–0.151, Table 3) for the best random-effect model (see online Appendix S2, Table S4 for details on model selection). We identified data quality and the reference pairing class as the main methodological moderators of r_{before} (see model selection on methodological moderators, online Appendix S2, Table S5). Mean r_{before} was positive when divorced birds were compared to faithful and to widowed birds (to faithful 0.173; 95% CI: 0.013–0.323, to widowed 0.181; 95% CI: 0.019–0.330), but not significantly different from zero if they were compared to the population mean (Figs 3B, 4A). In other words, birds that later divorced showed lower breeding success in the season before divorce compared to both faithful and widowed birds, but did not have different success than the population mean. Although dichotomisation was not selected in the final methodological moderators model, there was an indication of an interaction between dichotomisation and clutch size affecting the correlation between breeding success before divorce and divorce (i.e. model with the interaction was better supported than the model with only dichotomisation, see online Appendix S2, Table S5). Dichotomisation might decrease the effect size more strongly in species with larger clutch sizes (−0.025; 95%CI: −0.055–0.004).

As expected, we found that different stages of the breeding cycle (expressed at the highest hierarchical level, defined in Table 1) showed different effect sizes (controlled for the random effects of 'population' and 'phylogeny', and methodological moderators, see online Appendix S2, Table S6). Timing (laying date) and clutch size showed very similar (and positive) effect sizes ($r_{\text{before}} = 0.226$; 95% CI: 0.055–0.382 for timing; $r_{\text{before}} = 0.231$; 95% CI: 0.061–0.391 for clutch size),

Table 3. Effect sizes with 95% confidence intervals for the relationship between divorce and breeding success obtained by the best random-effect model for three separate meta-analyses (breeding success measured before divorce, as a change in success, or after divorce). Positive values of *r* correspond to the expected relationship between breeding success and divorce if divorce was an adaptive strategy. pMCMC is the *P*-value calculated in MCMCglmm for the intercept

Subset of data	Best random-effect model	Posterior mean	Lower/upper 95% CI	pMCMC
Before	Population	0.108	0.067/0.151	<0.001
Change	Population + phylogenetic tree	0.100	−0.176/0.353	0.390
After	Population + phylogenetic tree	−0.110	−0.191/−0.031	0.009

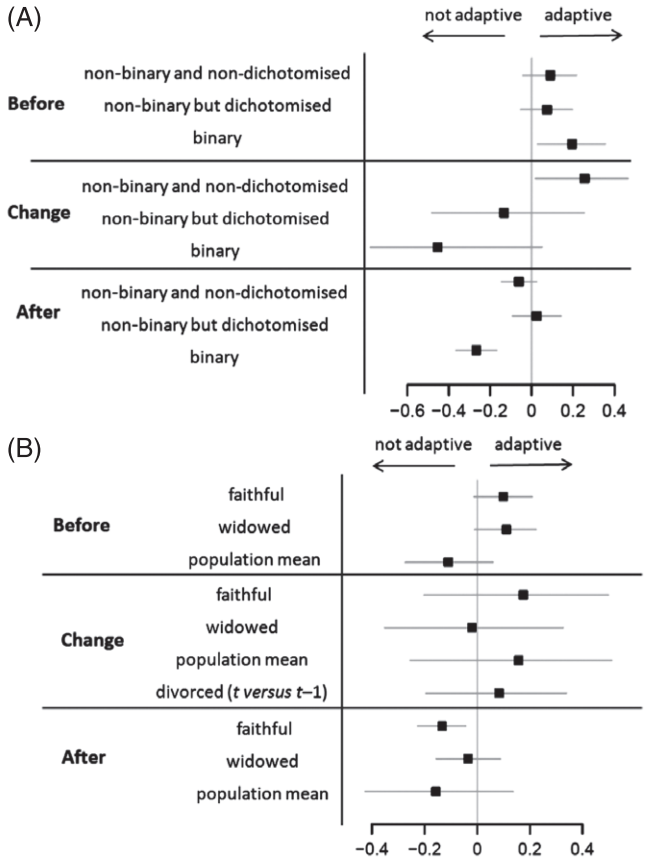

Fig. 3. Forest plots of the effect-size estimates (squares) and 95% CI (horizontal lines) for the relationship between divorce and breeding success for three separate meta-analyses (when breeding success was measured before divorce, as a change in success, or after divorce) according to: (A) type of dichotomisation; (B) reference pairing class. Positive values of r indicate the expected relationship between breeding success and divorce if divorce was an adaptive strategy.

while other stages showed no effect on divorce (i.e. all of the 95% CI overlapped zero, Fig. 4A). There was no support for any difference in effect sizes for studies which controlled for age and the ones which did not control for age (neither when included as an additive covariate, nor when included as interaction with the stage of breeding cycle, see online Appendix S2, Table S7). Similarly, there was no indication that effect sizes were influenced by the developmental mode of the species (see online Appendix S2, Table S8). We did not find any support for our predictions about the influence of species longevity and coloniality on the effect size (controlled for random effects and methodological moderators; both with, and without, controlling for clutch size, see online Appendix S2, Table S9). Similarly, there was no support for the influence of site fidelity, rate of extra-pair paternity of the species, and divorce rate of the population on r_{before} (see online Appendix S2, Table S10). Models including the continuity of partnership did not manage to estimate all of the parameters. Note that analyses of the influence of the last four factors were carried out on the subset of data for which we had information on the variables of interest.

Overall our results are consistent with the suggestion that birds use breeding success as a cue to divorce their partners, and that the strength of the response to low breeding success depends on the stage of the breeding cycle. More specifically, poorer performance at earlier stages of the breeding cycle (laying date and clutch size) seemed to be the main predictors of divorce.

(2) Correlation between divorce and change in breeding success

The effect size r_{change} represents the strength of the correlation between the change in breeding success and the occurrence of divorce. We found that the overall mean r_{change} was not significantly different from zero ($r_{\text{change}} = 0.100$; 95% CI: −0.176–0.353) for the best random-effect model (see online Appendix S2, Table S11 for details on model selection). However, inclusion of the term 'dichotomisation' (identified by model selection as the main methodological moderator of the effect size, see online Appendix S2, Table S12) revealed that this pattern was largely driven by species that lay only one egg and when otherwise non-binary success was dichotomised, the mean r_{change} was not significantly different from zero (Figs 3A, 4B). On the other hand, non-binary non-dichotomised data showed a positive effect size ($r_{\text{change}} = 0.256$; 95% CI: 0.018–0.467). These results caution against dichotomisation of breeding success in species with more than one egg when exploring the reproductive benefits of divorce.

Results of modelling the influence of the stage of the breeding cycle on the effect size were indicative of breeding success of some stages improving more (in terms of the 95% CI of the effect sizes), with the support for the model with and without the stage of the breeding cycle (expressed at the highest hierarchical level, Table 1) being similar in terms of the DIC values (Table 4; see online Appendix S2, Table S13). The occurrence of divorce correlated positively with advancement in the timing of breeding and with an increase in brood size (Fig. 4B). Furthermore, when we tested if the effect size depended on whether breeding success was measured for females, males, or both sexes combined, model selection revealed that the effect sizes differed between females and males (Table 4; see online Appendix S2, Table S14). Females improved egg laying date and brood-level components of breeding success, while males did not show any improvement (i.e. all effect sizes close to zero, 95% CI overlapped zero, Fig. 5). Females showed especially pronounced improvement at the brood level ($r_{\text{change}} = 0.637$; 95% CI: 0.328–0.817); this was the highest of all effect sizes obtained in our study. There was no support for a difference between studies which controlled for age and those

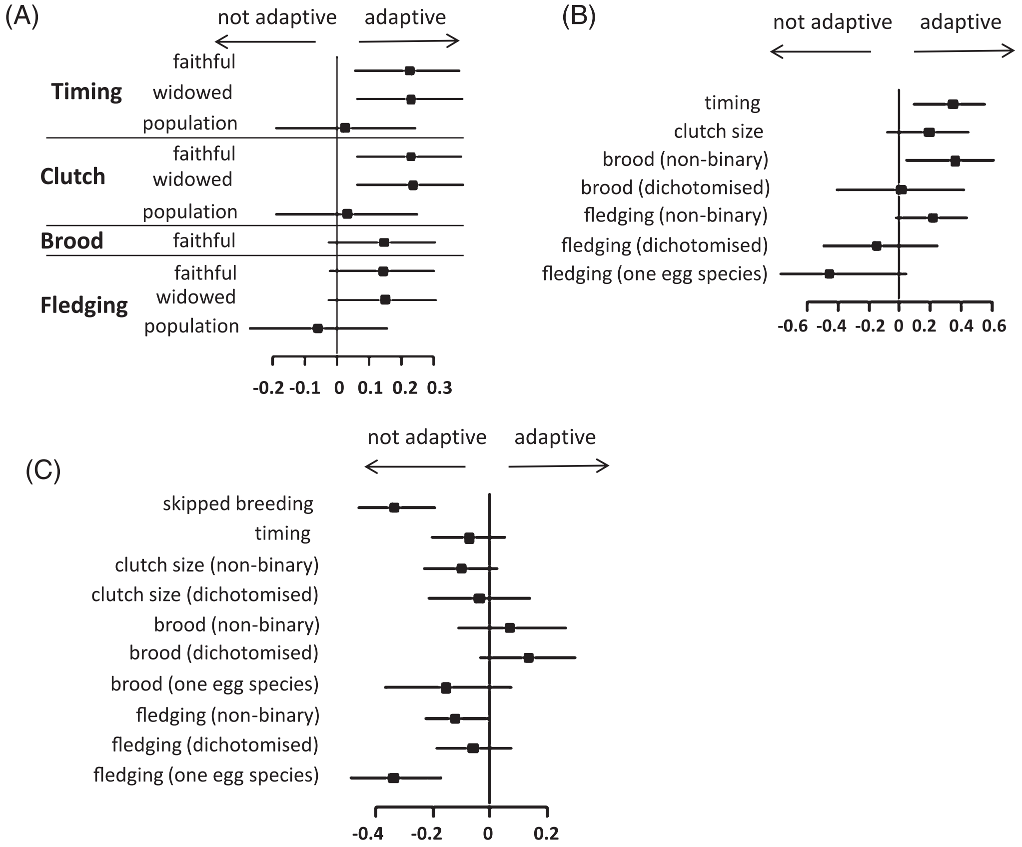

Fig. 4. Forest plots of the effect-size estimates (squares) and 95% CI (horizontal lines) for the relationship between divorce and the stage of a breeding cycle success was measured at, when: (A) breeding success was measured before divorce (given the group to which divorced birds were compared, controlled for data quality). Positive values of r correspond to divorced birds having lower breeding success compared to other groups. (B) Breeding success was measured as a change in success (given the dichotomisation of breeding success). Positive values of r correspond to divorced birds improving in breeding success. (C) Breeding success was measured after divorce (according to the dichotomisation and given for comparison of divorced birds to faithful ones). Positive values of r correspond to divorced birds having higher breeding success compared to other groups.

that did not (see online Appendix S2, Table S15), or a difference between species of different developmental mode (see online Appendix S2, Table S16). We did not find any support for an influence of life-history traits on the effect size. Inclusion of longevity and coloniality (both with and without controlling for clutch size) to the model with the fixed effect of dichotomisation did not change the DIC values, with the 95% CI overlapping zero (see online Appendix S2, Table S17). There was also no support for an influence of site fidelity, rate of extra-pair paternity, and divorce rate on r_{change} (see online Appendix S2, Table S18). Models including the continuity of partnership did not manage to estimate all of the parameters. Again, the influence of these last four factors was tested on subsets of data.

Overall, our results are supportive of divorce being correlated with reproductive benefits (i.e. an increase in breeding success between the two seasons), but detecting the effect was dependent on the methodological approach (breeding success was found to improve only when breeding success was not dichotomised). Moreover, we found that only females, and not males benefited from divorce.

(3) Correlation between divorce and breeding success in the season after divorce

Our final analysis was on the correlation between divorce and breeding success after divorce, r_{after}. As expected, the overall mean effect size, according to the best random-effect model in the set (Table 3) was negative ($r_{\text{after}} = -0.110$; 95% CI: -0.191 to -0.031), and remained similar in models with different random structures (see online Appendix S2, Table S19). In other words, divorced birds did less well than other birds in the season after divorce. However, incorporation of the two main methodological moderators (i.e. dichotomisation and the reference pairing class for divorced birds, identified by model selection, see online Appendix S2, Table S20) showed that divorced birds had

Table 4. List of models with corresponding DIC values testing for the influence of biological variables (i.e. stage of breeding cycle when breeding success was measured, and whether success was measured for individuals, males, or females) for three separate meta-anlyses (breeding success measured before divorce, as a change in success, or after divorce). First model in each meta-analysis is the best methodological moderator model (before mm = type of comparison + data quality; change mm = dichotomisation; after mm = type of comparison + dichotomisation). The random-effect structure for all of the models is: 'population' + 'phylogenetic tree'. ΔDIC is the difference between the DIC value of the main model (methodological moderators) and the model with the biological variable of interest

Meta-analyses	Biological variable tested for	Fixed-effect structure of the model	DIC	ΔDIC
Before		Before mm	−644.203	—
	Stage of breeding cycle	Breeding stage + before mm	−654.980	10.777
Change		Change mm	79.862	—
	Stage of breeding cycle	Breeding stage + change mm	82.953	−3.09
	Measured for individuals, males or females	Measured for + change mm	72.847	7.015
		Measured for × breeding stage + change mm	69.683	10.179
After		After mm	−7.412	—
	Stage of breeding cycle	Breeding stage + after mm	−6.590	−0.822
	Measured for individuals, males or females	Measured for + breeding stage + after mm	−2.644	−4.768
		Measured for × breeding stage + after mm	3.500	−10.912

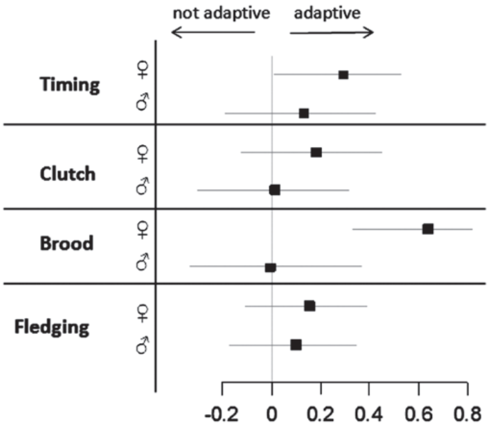

Fig. 5. A forest plot of the effect-size estimates (squares) and 95% CI (horizontal lines) for the relationship between divorce and change in breeding success for males and females, obtained by the model 'measured for' × 'breeding success measure' + dichotomisation. Reported are the values of the effect sizes for non-dichotomised breeding success. Positive values of r indicate the expected relationship between breeding success and divorce if divorce was an adaptive strategy.

lower breeding success only when compared to faithful birds ($r_{\text{after}} = -0.094$; 95% CI: −0.184 to −0.002, Fig. 3B). Breeding success was similar between divorced and widowed birds (i.e. 95% CI for r_{after} overlapped zero; Fig. 4B). These results indicate that both divorced and widowed birds suffer the costs of partner change.

There was no evidence that comparing breeding success at different stages of the breeding cycle between divorced birds and the reference pairing class influenced the effect size, with the DIC values being similar between models with and without this variable (Table 4; see online Appendix S2, Table S21). However, model results were indicative (in terms of 95% CI of the effect sizes) of a stronger negative effect of divorce on some components of breeding success, especially the cost of skipped breeding and failure to fledge a chick in species producing only one egg (Fig. 4C). There was no indication the effect sizes were influenced by the developmental mode of the species (see online Appendix S2, Table S22). Similarly, there was no support for the effect sizes being different for males and females (Table 4; see online Appendix S2, Table S23). Inclusion of species longevity and coloniality, both with and without controlling for clutch size, to the model structure of the best model as selected in the first two steps (random effects and methodological moderators) did not change the DIC values, with the 95% CI overlapping zero (see online Appendix S2, Table S24). There was also no support for the influence of site fidelity, rate of extra-pair paternity, and divorce rate on r_{after} (see online Appendix S2, Table S25). Models including the continuity of partnership did not manage to estimate all of the parameters. Again, the influence of these last four factors was tested on subsets of data.

Overall, the results of the analysis warn against comparing breeding success of faithful and divorced birds in the season after divorce when exploring possible benefits of divorce. Both widowed and divorced birds suffer a general short-term cost of partner change in terms of breeding success, and this masks signs of the improvement in breeding success of divorced birds. However, divorce is still costly, especially in terms of skipped breeding, and failing to fledge a chick in species with only one egg.

(4) Divorce *versus* any partner change – support for adaptiveness of divorce

Meta-analysis of the data set that encompassed the effect sizes of the relationship between breeding success and

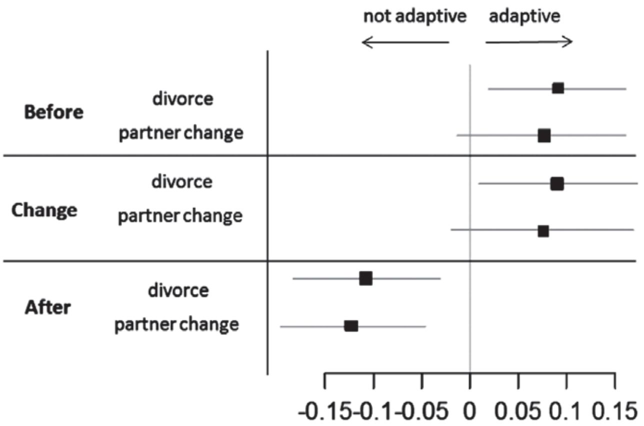

Fig. 6. A forest plot of the effect-size estimates (squares) and 95% CI (horizontal lines) for the relationship between divorce/partner change and breeding success, when breeding success was measured at $t-1$ (before), t (after), or as a change of success between the two (change). Positive values of r indicate the expected relationship between breeding success and divorce if divorce was an adaptive strategy.

divorce and breeding success and partner change (both widowed and divorced pairs/individuals) showed that r_{before} and r_{change} were significantly positive if breeding success was contrasted between divorced birds and the reference pairing class, but smaller and not significantly different from zero when success was contrasted between birds that changed partner and the reference pairing class (Fig. 6). The effect size r_{after} was more negative for the partner change than for divorce. Details on model selection are given in Appendix S2, Table S26. These results point towards divorce being less costly than partner change in general (i.e. both divorce and widowing), supporting the hypotheses that divorce is an adaptive strategy.

(5) Publication bias

Studies with statistically significant results are more likely to be published and therefore, particularly for studies with small sample sizes, larger effect sizes are likely to be over-represented (Palmer, 2000; Gates, 2002). To detect whether there was publication bias in our data set we conducted trim and fill analysis (Duval & Tweedie, 2000) and tested for the asymmetry of funnel plots for r_{before}, r_{change} and r_{after}. We performed trim and fill analyses in the 'metafor' package in R (Viechtbauer, 2010) using random-effect meta-analysis with restricted maximum-likelihood estimation (REML). As it is not currently possible to perform trim and fill algorithms in Bayesian mixed models, we were not able to account for the non-independence of data from the same population or species. To attempt to overcome this problem, we also conducted trim and fill analyses on data sets with one randomly chosen effect size per population, and repeated the randomisation followed by the trim and fill procedure 1000 times (for an example of a funnel plot when one effect size per population was used see Fig. 7; and Appendix S2, Fig. S9 when all the effect sizes were used). We report the median number of missing studies, and average of the estimated effect sizes with associated S.D. of the 1000 estimates (see online Appendix S2, Table S27). There was no evidence that effect sizes were influenced by a small-population effect in any of our data sets. When multiple effect sizes were included per population (i.e. when the analysis was run on the overall data set), the estimated number of missing points was 15 for r_{before} (estimated effect size 0.124; 95% CI: 0.097–0.152), 0 for r_{change}, and 23 for r_{after} (estimated effect size −0.170; 95% CI: −0.219 to −0.055). When a randomly chosen effect size per population was used, the median estimated number of missing studies was 0 for all of the data sets (see online Appendix S2, Fig. S10 for the frequency distribution of the estimated number of missing studies for 1000 runs). The average r_{before} (0.102; S.D. = 0.024), r_{change} (0.140; S.D. = 0.103), and r_{after} (−0.120; S.D. = 0.062) for all of the 1000 runs were similar to the r values obtained on the overall data set. We tested the funnel plot asymmetry using Egger's regression test (where the effect size is regressed on the effect standard error: Egger *et al.*, 1997). We used the model structure of the best random and methodological moderator model as selected in the primary meta-analyses (and with the same settings, i.e. priors, iterations, burn-in, thinning) for the 'before', 'change', and 'after' data sets (random structure for all analyses 'phylogenetic tree' + 'population'; fixed structures: 'before' data set, 'breeding stage' + 'reference pairing class' + 'data quality'; 'change' data set, 'measured for' + 'dichotomy'; 'after' data set, 'reference pairing class' + 'dichotomy') in MCMCglmm, with the S.E. as the covariate. The results showed that effects of small-sample studies did not have a significant influence on estimates of the effect size for r_{before} and r_{after} (95% CI overlap zero, pMCMC >0.49 and >0.62, respectively) supporting the results of the trim and fill analysis. Small-sample-size studies had marginally non-significantly positive influence on the effect size for r_{change} (pMCMC = 0.064). Hence, these analyses suggest that the patterns we report are robust to the issue of missing data.

V. DISCUSSION

Relating breeding success to the occurrence of divorce is the main approach used to test the adaptiveness of divorce. However, empirical evidence is varied both in terms of the direction and strength of effects (this study; Dubois & Cézilly, 2002). Herein, we tested the overall evidence for adaptiveness of between-season divorce

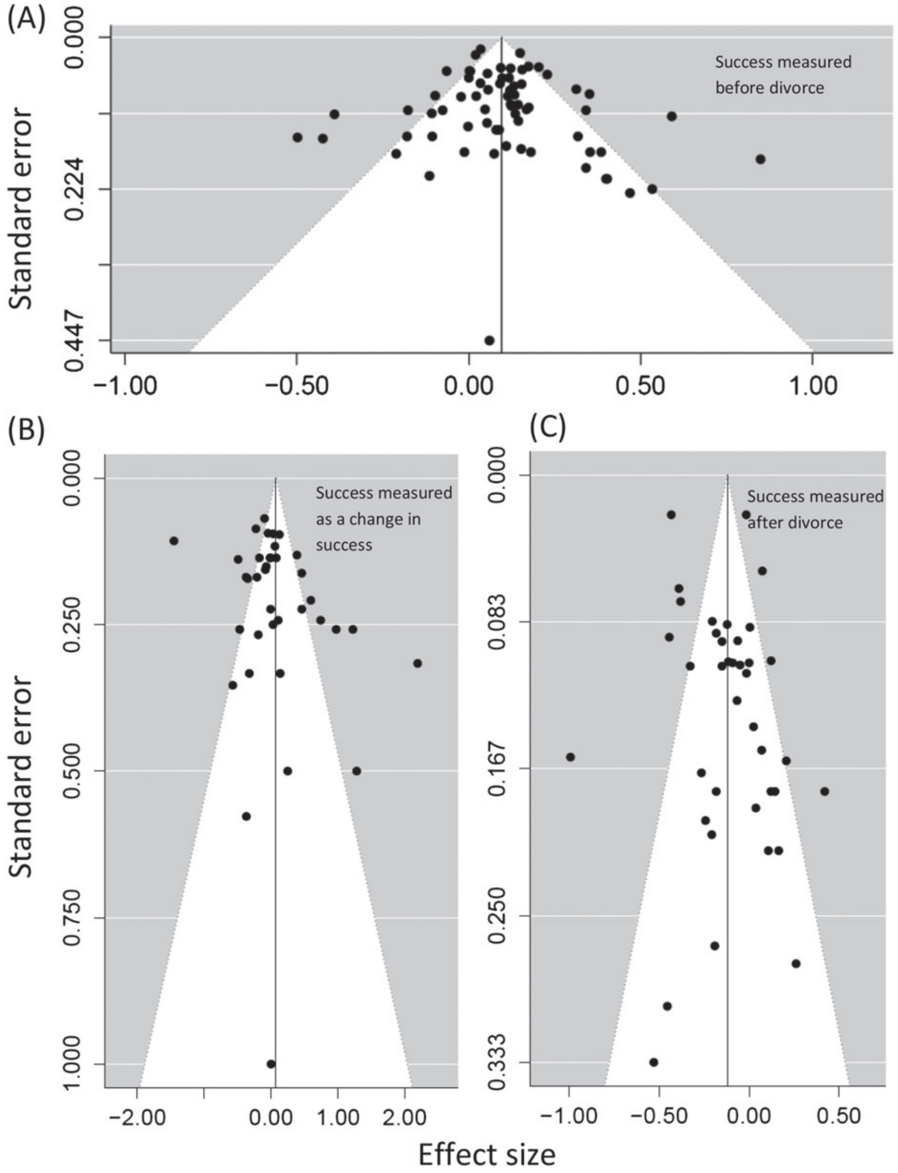

Fig. 7. Funnel plots (plots of the effect size *versus* the standard error of the effect) for the effect size of the correlation between breeding success and divorce in monogamous species on three different data sets. (A) Breeding success measured before divorce, (B) breeding success expressed as a change of breeding success between the two seasons, (C) breeding success measured after divorce only. Funnel plots are constructed using a randomly chosen effect size per population (see online Appendix S2).

in monogamous birds, and explored how biological factors and methodological approaches influenced the strength of the correlation between breeding success and the occurrence of divorce. To do this, we applied phylogenetic meta-analysis to a large number of studies that reported relationships between divorce and breeding success. Our study covered 64 monogamous bird species, while accounting for the dependence of multiple effect sizes within studies and the phylogenetic relatedness of studied species. A summary of the main hypotheses and findings of our meta-analyses is given in Table 5. Our results support the hypothesis that divorce is an adaptive strategy, because we show that: (*i*) birds that divorced had lower breeding success prior to divorce than other birds, and (*ii*) they improved their breeding success by divorcing. Although the overall effect sizes in our analyses were relatively weak ($r_{\text{before}} = 0.108$; 95% CI: 0.067–0.151, $r_{\text{change}} = 0.100$; 95% CI: −0.176–0.353, $r_{\text{after}} = -0.110$; 95% CI: −0.191 to −0.031), we showed the effect sizes to depend both on the methodological approaches used and on two biological variables (the stage of the breeding cycle and sex, Table 5). For example, while the overall r_{change} was not significantly different from zero, we found that after controlling for methodological moderators, females improved their breeding success strongly by divorce ($r_{\text{change}} = 0.637$; 95% CI: 0.328–0.817). This was the largest effect size we identified in all of our analyses. We emphasize that researchers should acknowledge the potential effect their methods might have on the results, which should be taken into account while designing their studies, and interpreting the results.

(1) Evidence that divorce is an adaptive strategy

The first evidence that divorce is an adaptive strategy in monogamous birds comes from our meta-analysis on the correlation between breeding success before divorce and the occurrence of divorce. The results of the analysis indicate that the decision to divorce is based on breeding success, with low breeding success triggering divorce (as suggested previously, e.g. Black, 1996; Dubois & Cézilly, 2002). More specifically, it seems that breeding success at earlier stages of the breeding cycle is an important driver of divorce (i.e. birds that will subsequently divorce between two breeding seasons started to breed later and had a lower clutch size in the first season compared to birds that remained faithful or were widowed). We offer two explanations as to why this might be the case. First, the influence of environmental stochasticity might be more pronounced at later stages of the breeding cycle (because its effects on breeding success might accumulate over different breeding stages), and parental ability to adjust to fluctuating environments might be more pronounced at earlier stages (see Lindström, 1999)– consequently, later stages are not selected for as drivers of divorce. Second, the level of investment in the relationship with the partner becomes higher at later stages of the breeding cycle. Consequently, the benefits of staying with a familiar mate in the next season become higher, leading to higher trade-offs between possible benefits of divorce and benefits of mate familiarity (Choudhury, 1995; Black, 1996). As a result, the response to lower breeding success is reduced at later stages. However, given the lack of current knowledge about the level at which individuals are able to judge their success (or the prospects for its improvement), explanations for these results remain speculative.

The second line of support that divorce is an adaptive strategy comes from our meta-analysis on divorce and change in breeding success, with divorce being correlated with an increase in breeding success between the two seasons. The strength of this relationship was highly dependent on sex and methodological moderators. First, we found evidence that females benefited from divorce, as they significantly advanced laying date, and the brood-level components of breeding success, while there was no increase in breeding success for males. Particularly interesting was the large increase in success at the brood level (percentage of eggs that produced hatchlings and number of hatchlings) females gained by divorcing. One possible explanation of this female-biased improvement is that females are more often the initiators of divorce (regardless of whether they seek a better mate, or better territory), as suggested by some authors (see Cézilly *et al.*, 2000*b*). If male involvement is an important factor at early stages of reproduction (feeding the female and providing food for hatchlings) as the results of some studies suggest (e.g. Sanz & Tinbergen, 1999; references in Galvan & Sanz, 2011) then females might benefit (i.e. increased number of hatchlings) from pairing with males of higher parental quality (and/or social status) for whom they divorce their former partners. Moreover, it has been shown that females invest in the clutch (both clutch size and egg size) as a response to male quality (Horvathova, Nakagawa & Uller, 2012), which may contribute to higher hatching success and number of hatchlings with the new partner. On the other hand, if females choose territories rather than males (Blondel, Perret & Galan, 2000; Garcia-Navas & Sanz, 2011) then an increase in territory quality after divorce would lead to an increase in the number of chicks. However, this does not exclude the possibility that this effect results from females choosing males, as males of higher quality frequently hold better territories (Hoileitner, Nechtelberger & Hoi, 1995; Wolfenbarger, 1999). Insufficient data on territory quality were available to test for effects of territory quality on divorce. In addition, inclusion of the male contribution to parental care might help to discriminate if paternal care is an important factor contributing to the differences in divorce rates among species. However, current data on paternal investment for different species is still of insufficient quality and precision to perform any comparison (A. S. Griffin, personal communication). Costs related to change of territory (which frequently accompanies partner change, e.g. Andreu & Barba, 2006, and references therein) might also be a part of the reason for the absence of an improvement in breeding success in divorced males. As males establish and defend territories more often than females (Schjorring, Gregersen & Bregnballe, 2000), the additional costs of territory change for males might lead to the absence of selection on males as initiators of divorce, or/and mask any possible improvement in breeding success if divorced males also change territories. Again, insufficient data on territory change was available to test for effects of territory change and divorce on breeding success of males and females. Experimental approaches (e.g. manipulating the availability of males or sites of different qualities) would be the best way to discriminate between the importance of male and territory quality (e.g. Alatalo, Lundberg & Glynn, 1986; Beguin *et al.*, 2006; Sirkia & Laaksonen, 2009; Jacot, Valcu & Kempenaers, 2010).

Table 5. Summary of the main predictions and findings of the meta-analyses on the correlation between breeding success and divorce in monogamous birds

			Influence of the moderators on the effect size (r)				
When breeding success was measured	Prediction if divorce is an adaptive strategy	Support for the hypotheses found[a]	Methodological moderators[b]	Stage of breeding cycle[c]	Sex	Life-history traits[d], extra-pair broods, divorce rates	Covariates in the best supported model[e]
Before divorce ($t-1$)	Low breeding success triggers divorce	Yes	Divorced birds have lower breeding success than faithful and widowed birds, r decreases with the increase in data quality	Laying date and clutch are precursors to divorce, other stages not	Not tested	No	Stage of breeding cycle + reference pairing class + data quality
Change in breeding success between two breeding seasons	Breeding success of divorced improves more than others	Yes	Not dichotomised breeding success show positive change, binary and dichotomised breeding success show no change	Laying date and brood level measures improve, other stages do not	Females benefit from divorce, males do not	No	Sex × stage of breeding cycle + dichotomisation
After divorce (t)	Not relevant	—	Divorced birds do worse than faithful, but no worse than widowed, dichotomisation influences r	Yes – main costs of divorce: skipped breeding, not fledging a chick in species with one egg	No difference between sexes	No	Reference pairing class + dichotomisation
All of the above temporal contrasts	Divorce compared to partner change[f]: stronger response to low breeding success, more positive change in breeding success; less worse breeding success compared to faithful birds in t	Yes	Not tested	Not tested	Not tested	Not tested	Partner change or divorce + temporal contrast

[a] One or more effect sizes of the best model is significantly greater than zero.

[b] Methodological moderators: data quality, dichotomisation (levels: binary, non-binary but dichotomised, and non-binary and non-dichotomised), reference pairing class (faithful, widowed, population mean, comparison of breeding success at $t-1$ and t for divorced).

[c] Stage of breeding cycle: skipped breeding, timing, clutch size, brood, fledging.

[d] Longevity and coloniality, controlled for clutch size.

[e] Out of the models tested, all have the same random structure of 'population' and 'phylogeny'.

[f] Partner change can happen both because of divorce or because of widowing. Some studies do not distinguish between the two and report the values for this more general category only.

Finally, it is important to emphasise that the effect size of the correlation between divorce and change in breeding success was significant only when breeding success was non-binary and non-dichotomised ($r_{\text{change}} = 0.256$; 95% CI: 0.018–0.467), while the 95% CI for binary and dichotomised measures overlapped zero. This result suggests that dichotomisation of non-binary measures of breeding success, like the change in the number of eggs/chicks in species with clutch sizes greater than one egg, potentially masks the effects of divorce (also see Dubois & Cézilly, 2002). This would especially be the case when complete breeding failure (no success at all) is more likely to be the result of stochastic environmental effects such as predation or extreme weather rather than parental quality.

(2) Challenges in estimating post-divorce success

Although we found that, in the season after divorce, divorced birds did worse than others (i.e. had lower breeding success), this does not mean that divorce was not adaptive. First, when the breeding success of divorced birds prior to divorce is lower than the breeding success of others (as found in this study), divorced birds may still improve more than other birds between the two seasons, while their breeding success after divorce remains lower than the breeding success of faithful birds. This would mask an improvement in breeding success between the two seasons when only measuring breeding success after divorce. Second, there might be costs of partner change (e.g. one partner is inexperienced with the site, or the coordination between pair members is suboptimal, Cooke, Bousfield & Sadura, 1981; Linden, 1991; Choudhury & Black, 1994; Naves, Cam & Monnat, 2007) which obscure the signs of improvement if breeding success is measured and compared to faithful birds in the breeding season after divorce only (Choudhury, 1995). Our meta-analysis supported this suggestion as we found that divorced birds did less well than faithful ones, but had similar success to widowed birds. Moreover, the difference in breeding success was larger between birds that changed partner (both due to widowing and divorce) and faithful birds, than between divorced and the other birds. These two results suggest that for divorced birds the costs of partner change were, at least partly, compensated by an improvement of breeding success. However, costs of partner change are present; perhaps the most substantial cost is skipping breeding, as we identified in our analysis. We may well have underestimated the cost of skipping breeding as in many species non-breeding individuals were not detected as non-breeders (but considered dead). Interestingly, as the majority of effect sizes for skipped breeding in our data set come from the comparison of its occurrence between divorced and widowed birds, our results suggest that divorced birds skip breeding more often than widowed ones. As suggested by the residual reproductive value hypothesis (e.g. Coulson, 1984; Aebischer & Wanless, 1992), skipping breeding might be a choice given the trade-off between current and future reproduction. If so divorce participants might choose to skip breeding (which consequently led to divorce), while widowed birds still try to breed after mate loss. It might also be that divorce participants are birds of lower quality (Bruinzeel, 2007), and once without a partner, have less chance to obtain a new one compared to widowed birds. We also found that species with only one egg suffer more from divorce than other species, as the fledging success of their offspring is more reduced. As in our data set these species also tend to be long-lived, benefits might become apparent after a few years. Consequently, we suggest measuring breeding success over several breeding seasons in those and other long-lived species.

We would also like to emphasise that breeding success is just one component of fitness. Results of a few studies suggest that divorce (and other forms of partner change) might also negatively affect survival (Nicolai *et al.*, 2012; Culina *et al.*, 2013). If this is the case, studies on the correlation between breeding success and divorce use only the subset of individuals that have survived the change of partner and therefore underestimate the effect of divorce on fitness. We are aware that determining if an individual has died between the two breeding season because it divorced would require detailed observations through the non-breeding period. However, it is still important to acknowledge the possibility of the presence of survival costs to divorced birds when discussing the adaptiveness of divorce.

(3) Life-history moderators of selection on divorce

Although theory (and several comparative studies) suggest that both longevity (e.g. Williams, 1966; Stearns, 1992; Erikstad *et al.*, 1998) and coloniality (e.g. Dubois *et al.*, 1998; Jeschke & Kokko, 2008), should affect the costs and benefits of divorce, we found no support for this in any of our meta-analyses. Wide confidence intervals for the effects of these variables might be indicative of the heterogeneity of the additional costs (or benefits) of coloniality and longevity to divorce, which could also largely depend on other life-history traits (e.g. migration pattern) or population-specific factors. For example, while in non-migratory species our prediction on the correlation between longevity and effect size might hold (i.e. long-lived species benefit less from divorce), in migratory species there might be no such correlation because waiting for the partner that might be already dead might be equally costly regardless of longevity. Including additional data on life-history traits of different species or on population-specific demographic factors which interact with longevity or coloniality might elucidate their effect on the relation between divorce and breeding success. Second, differences in methodological approaches to studying breeding success in long-lived colonial species and short-lived species (e.g. in long-lived colonial species nests are usually easier to locate and pair members are identified at earlier stages of reproduction) might also influence our ability to detect differences in costs and benefits of divorce among species with different life histories.

We also did not detect any effect of site fidelity on the effect size in any of the meta-analysis; this could be related to an oversimplification of site fidelity by the measure we used. Additional data on exact rates of site fidelity, variation of site fidelity among different populations of the same species, as well as sex-specific rates of site fidelity should be explored. Similarly, our inability to detect any effect of developmental mode on the effect size could be due to the lack of more accurate data on the importance of parental care at different stages of chick development.

(4) Methodological advice for future studies

Based on the results of our analyses, we suggest the following should be considered in future empirical studies on the adaptiveness of divorce: (*i*) measuring success after divorce only could be misleading as partner change (but not divorce *per se*) might be costly; (*ii*) the breeding success of divorced birds should be compared to both faithful and widowed birds, to separate the costs of divorce from the costs of partner change, especially if breeding success was measured only in the season after divorce; (*iii*) measure the change in the exact numbers of eggs/chicks/fledglings for species with more than one egg, as the increase in number of eggs/chicks might better reflect the benefits of divorce; (*iv*) measure breeding success over multiple years for long-lived species (especially those that produce only one egg). In the first year(s) after divorce costs of divorce and partner change might outweigh the benefits, but benefits might become apparent after a few years; (*v*) recording the age of divorce participants. Age often correlates to breeding success and might therefore affect the costs and benefits of divorce. Also future breeding opportunities might vary with age, which would result in age-dependent divorce strategies. Finally, recapture might also depend on age, and thus bias the effect sizes; (*vi*) recording birds changing territories as well as the quality of those territories. This would partly enable the disentangling of the correlating effects of divorce and territory change on breeding success.

VI. CONCLUSIONS

(1) Understanding ultimate fitness costs and benefits of divorce can greatly help to understand the evolution and emergence of mating systems, and patterns of population dynamics. We gathered empirical evidence on the correlation between breeding success and occurrence of between-season divorce in monogamous birds, and showed that the evidence supports the conclusion that divorce is an adaptive strategy to improve reproductive situations.

(2) In agreement with the findings of the previous meta-analysis on the correlation between divorce and prior breeding success (Dubois & Cézilly, 2002), we found that low breeding success triggers divorce. We also showed, to our knowledge for the first time, that there is overall evidence that divorce is also correlated with an increase in breeding success between two breeding seasons in species that produce more than one egg.

(3) We highlight the importance of choosing an appropriate study design to test for adaptiveness of divorce, as results depend greatly on the approach used. We recommend measuring breeding success not only after divorce but also before, comparing breeding success to both widowed and faithful birds to separate the costs of divorce from the costs of partner change and, whenever possible, measuring the exact numbers of eggs, chicks or fledglings rather than measuring only breeding failure *versus* success.

(4) We believe that our study establishes the previously suggested hypothesis that divorce is an adaptive behavioural strategy to increase breeding success in monogamous birds. As such, it provides ground for further investigation of external covariates affecting divorce (e.g. social and ecological factors) as well as more in depth analysis of the mechanisms underlying the differences in the effect sizes of the proximate fitness causes and consequences of divorce. Finally, we advocate that studies should also aim to explore whether divorce influences survival, as both survival and breeding success determine the final fitness of an individual.

VII. ACKNOWLEDGEMENTS

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VIII. REFERENCES

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Full data set used in each meta-analysis, including information on life-history traits of the species (Tables S1 and S2).

Appendix S2. Additional information on data quality assessment, calculation of the effect sizes, and additional results tables (Tables S3–S27).

SUPPORTING INFORMATION

Trading up: the fitness consequences of divorce in monogamous birds

Antica Culina, Reinder Radersma and Ben C. Sheldon

I. METHODS

(1) Assessing data quality

We considered the following components when assessing data quality for each data point (i.e. each effect size).

(*a*) If different sources within the paper reported different values for the same component (or components) necessary to calculate the effect size (e.g. sample sizes reported in figures and the main text did not match), we scored the data point as 1 or 2, depending on how large the mismatch was (and how strongly this would influence the final effect size).

(*b*) If the sample size was only possible to calculate indirectly (i.e. sample size was not provided as a single value by the authors, but inferred from other information within the paper), we scored the data point as value 1 or 2, depending on the amount of indirect information needed to calculate the effect size (two sources of information needed = 2, more than two sources of information needed = 1).

(*c*) For studies reporting both the raw data and the corresponding test statistics, if the effect sizes calculated from both of these differed by less than 0.01, than we assigned value 3 to the effect size. If the difference was more than 0.01 we assigned value 1, 2 or 3 to the effect size, depending on whether one source (e.g. test statistics), was obviously wrongly reported/calculated in the study, while the other source (e.g. raw data) seemed fully correct (assessed using points *a* and *b*).

(2) Calculating the effect sizes

For each data point, we first calculated the effect size as a Pearson's correlation coefficient, *r*, using either the 'raw' values reported in the paper (mean and error of breeding success of contrasted pairing classes, i.e. divorced, faithful, widowed; or contingency table, i.e. number of successes/failures in a certain pairing class given breeding success measure) or the corresponding test statistics (together with sample size and the direction of the effect).

There were three main ways studies addressed the correlation between breeding success and the occurrence of divorce.

(*i*) The first approach is to compare breeding success between birds that divorce (will divorce, or are already divorced) and the reference pairing class (which can be faithful birds, widowed birds, or population mean), or to compare breeding success a bird achieved after divorce to its breeding success before divorce. These studies sometimes report only the raw values of breeding success (i.e. mean and error measure), sometimes only the corresponding test statistics, and sometimes both of these.

(*ii*) The second approach is to compare the numbers of birds that failed/succeeded in each of the two pairing classes that are contrasted ('contingency table' form of data). Breeding success measure is in this case always either binary or dichotomised. Again, these studies report either the raw values (i.e. number of birds in each category), or the related test statistics (or both).

(*iii*) The third approach is to report the correlation coefficient between divorce and breeding success (only a small number of studies in our data set were in this group).

When studies presented data as figures, we used the program TechDig (Jones, 1998) to extract the values of breeding success [usually the mean with 95% confidence intervals (CI), standard errors (S.E.), or standard deviations (S.D.)] from the graph.

(*a*) *Data reported as a test statistics*

When data were reported in a form of the test statistics, we used the following formulae to convert them into the Pearson's correlation coefficient (*r*):

Test statistics	*r*
Z *	$Z/\sqrt{N}$
F	$\sqrt{\frac{F}{F+\text{d.f.}}}$ **
t	$\sqrt{\frac{t^2}{t^2+\text{d.f.}}}$ ***
χ^2	$\sqrt{\frac{\chi 2}{N}}$
LRS	$\sqrt{\frac{LRS}{N}}$
Mann-Whitney *U*	$1–2\times U/(n_1\times n_2)$

**Z* can be either the standard normal, or *Z* from the Mann-Whitney *U* test.
** d.f. = degrees of freedom of the error term ($N–K$).
*** d.f.=N–1 for paired design, and d.f.=N–2 for two-sample design.

Several studies provided *P*-values together with the sample size (or degrees of freedom). For these we calculated the value of the test statistics using the *P*-values and the sample size. If the study provided both *P*-values with sample size and the value of the test statistics, we checked that the value of the test statistics corresponded to the *P*-value and the sample size. If these did not match, we contacted the authors.

(*b*) *Data reported as means with error measures*

To calculate *r* directly from means and error measures, we used the following procedures and formulae:

First, we calculated Hedge's *g* as:

$$g = \frac{x1 - x2}{s}$$

where *s* is the pooled sample variance calculated as:

$$s = \sqrt{\frac{(n_1 - 1) * s_1^2 + (n_1 - 1) * s_2^2}{n_1 + n_2 - 2}}$$

and *x*1 and *x*2 are the means of the two groups (group 1 and group 2) that are compared, n_1 and n_2 are corresponding sample sizes, and s_1 and s_2 corresponding sample variances.

Next we used Hedge's *g* to calculate *r*. The formula we applied depended on whether the two groups (between which means were compared) were composed of different individuals (i.e. divorced birds *versus* faithful/widowed birds) or the same individuals (i.e. divorced birds before and after divorce). In the first scenario, we calculated *r* as:

$$r = \sqrt{\frac{g^2}{g^2 + \frac{\mathrm{d.f.}}{N * p_1 * p_2}}}$$

where $p_1 = n_1/N$ and $p_2 = n_2/N$, d.f.=N–2,

and in the second scenario as:

$$\sqrt{\frac{g^2}{g^2 + \frac{\mathrm{d.f.}}{N}}}$$

where d.f.=N–1.

(*c*) *'Contingency table' type of data*

When data were presented in the form of a contingency table, we calculated *r* using the formula:

$$r = \frac{A*D - B*C}{\sqrt{(A+B)(C+D)(A+C)(B+D)}}$$

where *A*, *B*, *C*, and *D* are the numbers of birds in each unique category of the contingency table.

If the study reported both the raw data and the related test statistics (161 effect sizes were ‘double’ reported), we calculated *r* from both of these sources. If the difference between the two was less than 0.01 (84 ‘pairs’ of effect sizes), than we kept the *r* value calculated from the raw data because more effect sizes in the overall data set reported this value (we calculated 234 effect sizes from the raw values only and 43 from the test statistics only). If the difference was more than 0.01, we contacted the authors or kept the value we trusted more (as explained above).

After we calculated the Pearson’s correlation coefficient, we transformed it into Fisher’s Z (Z_r) using the formula

$Z_r=0.5\times\ln[(1+r)/(1-r)]$.

We calculated the corresponding standard error as

S.E.$=1/\sqrt{N-3}$.

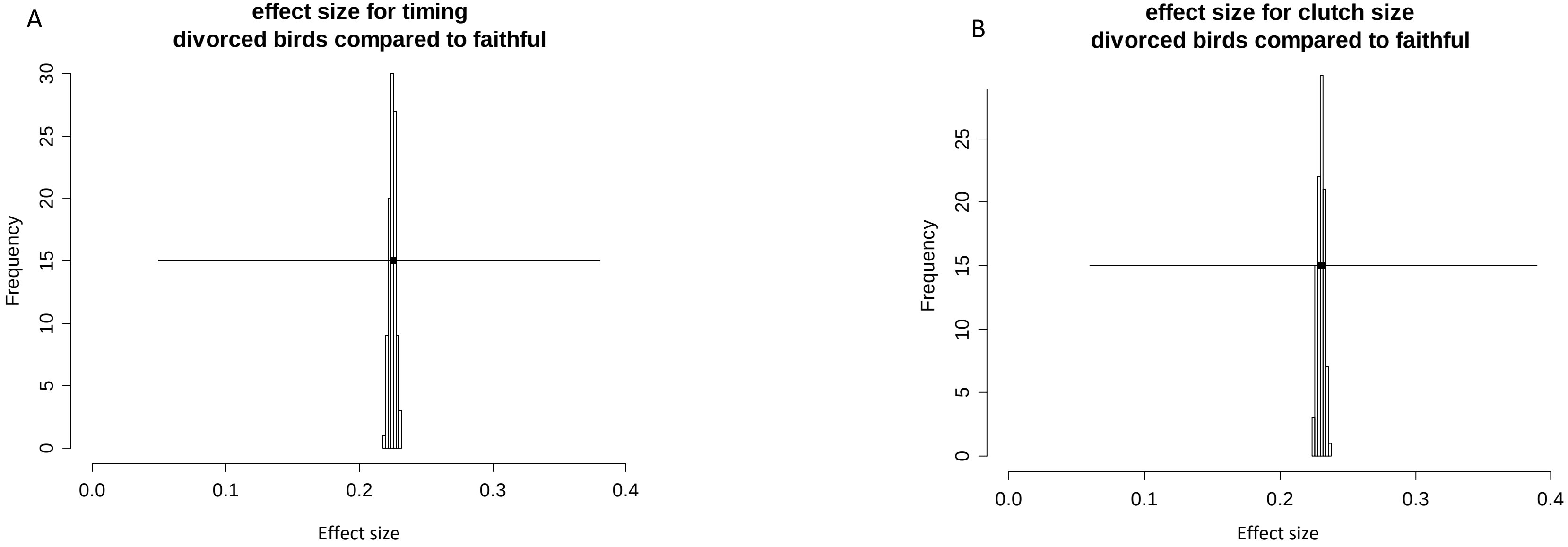
We used Z_r (which has a normal distribution) as the response variable in the meta-analyses.

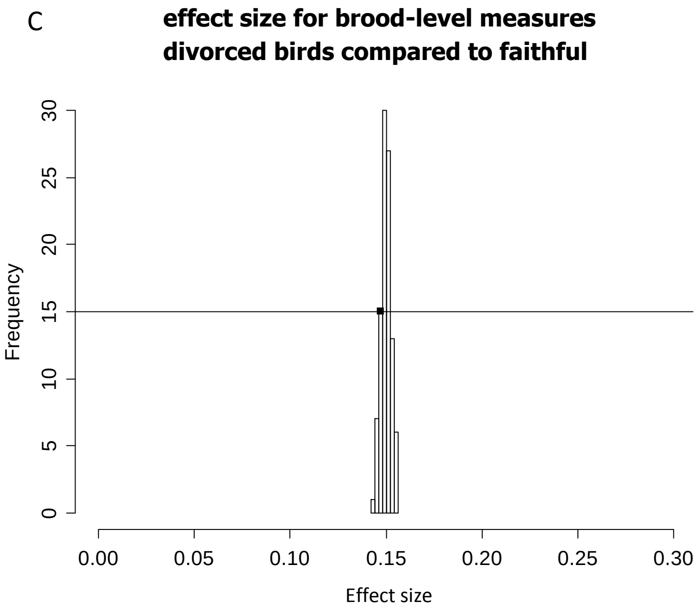
(3) Details of the trim and fill procedure

Studies with statistically significant results are more likely to be published and therefore, particularly for studies with small sample sizes, larger effect sizes are likely to be over-represented (Palmer, 2000; Gates, 2002). To detect whether there was a publication bias towards significant results in our data set we conducted a trim and fill analysis (Duval & Tweedie, 2000) and tested for asymmetry in the funnel plots for r_{before}, $\mathrm{r}_{\text{change}}$ and r_{after}. We performed the trim and fill analyses with the ‘metafor’ package in R (Viechtbauer, 2010), using random-effect meta-analysis with restricted maximum likelihood estimation (REML). Trim and fill analysis estimates the number of studies that are not published because of publication bias, and recalculates the effect size by adding simulated data points to the original data set. The ‘trim’ part of the method assumes that plots of the effect sizes *versus* their standard errors should be symmetrical if there is no bias. It identifies the effect sizes that make major contributions to the funnel plot asymmetry, and eliminates those estimates. The process is repeated until there are no more effect sizes left for which their removal significantly affects the average effect size. Next, the remaining effect sizes are used to estimate the true centre of the funnel. Finally, the ‘fill’ part of the method replaces ‘trimmed’ effect sizes by the same number of simulated effect sizes, producing the final estimate of the true mean and its variance based on the filled funnel plot. The statistical procedure involves an iterative resampling process (see Duval & Tweedie, 2000). As it is currently not possible to perform trim and fill algorithms on Bayesian mixed models, we were not able to account for the interdependence of the data coming from the same population or species. To partly overcome this problem, we also conducted trim and fill analyses on data sets with one randomly chosen effect size per population, and repeated the randomisation followed by the trim and fill procedure 1000 times (for an example of a funnel plot when one effect size per population was used see Fig. 2; and online Fig. S9 when all effect sizes were used). We report the median number of missing studies, and the average of the estimated effect sizes with the associated standard deviation for the 1000 estimates (online Table S25). The precise description of the R code is given in Viechtbauer (2010).

II. RESULTS

Figure S1. Histograms of the effect sizes (posterior mean *r* estimates) obtained for all 100 phylogenetic trees. Effect sizes were calculated for the best model of the meta-analysis on the correlation between breeding success before divorce and the occurrence of divorce. Squares (mean effect sizes) and error bars (95% CI) are the results of the best model, run on one randomly selected tree which we present in the main article. Structure of the model: ‘population’ + ‘phylogeny’ (random effects); ‘stage of breeding cycle’ + ‘reference pairing class’ + ‘data value’ (fixed effects). The histograms are given for the effect sizes when divorced birds are compared to faithful ones with respect to: (A) timing of breeding; (B) clutch size; (C) brood-level measures; (D) fledging-level measures.




C
effect size for brood-level measures
divorced birds compared to faithful
Frequency
0
5
10
15
20
25
30
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Effect size

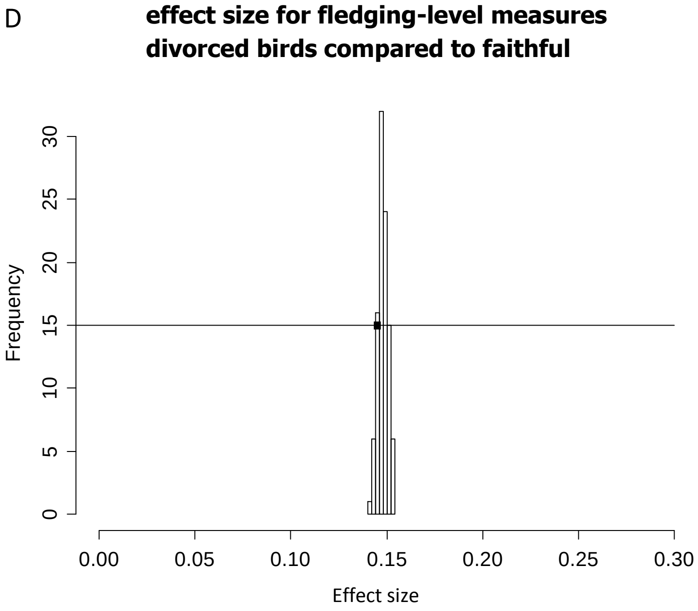
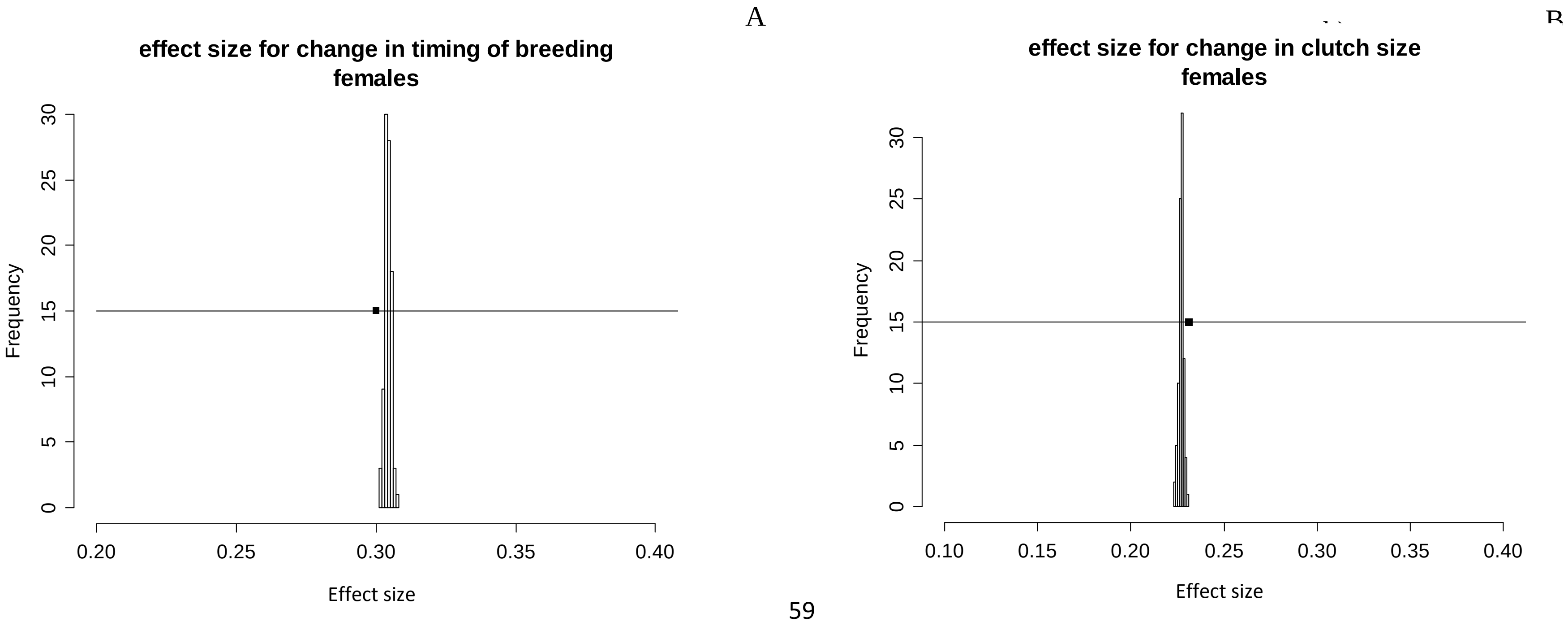
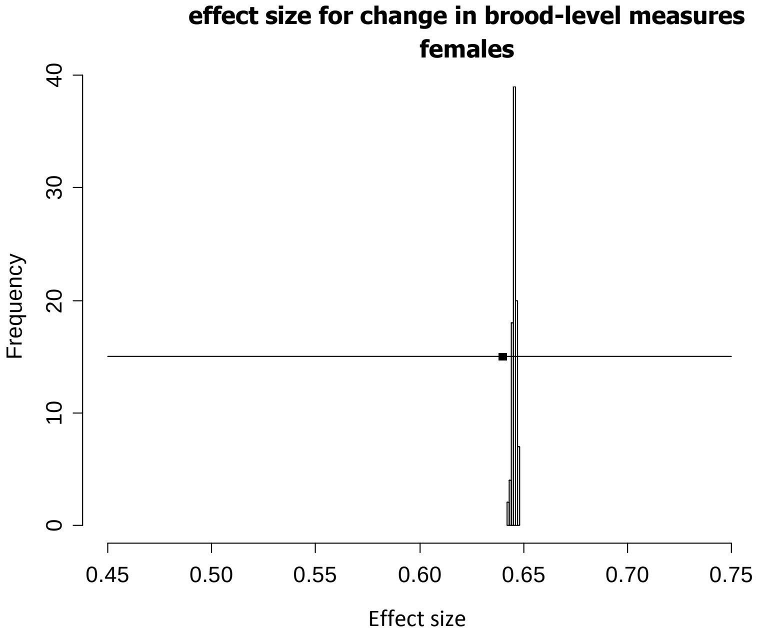

D
effect size for fledging-level measures
divorced birds compared to faithful
Frequency
0
5
10
15
20
25
30
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Effect size

Figure S2. Histograms of the effect sizes (posterior mean *r* estimates) obtained for all 100 phylogenetic trees. Effect sizes were calculated for the best model of the meta-analysis on the correlation between the occurrence of divorce and change in breeding success. Squares (mean effect sizes) and error bars (95% CI) are the results of the best model run on one randomly selected tree which we present in the main article. Structure of the model: 'population' + 'phylogeny' (random effects); 'stage of breeding cycle' + 'sex' + 'dichotomisation' (fixed effects). The histograms are given for change of breeding success in females when breeding success measure is not dichotomised: (A) timing of breeding; (B) clutch size; (C) brood-level measures; (D) fledging-level measures.



C


effect size for change in brood-level measures
females
Frequency
0
10
20
30
40
0.45
0.50
0.55
0.60
0.65
0.70
0.75
Effect size

D

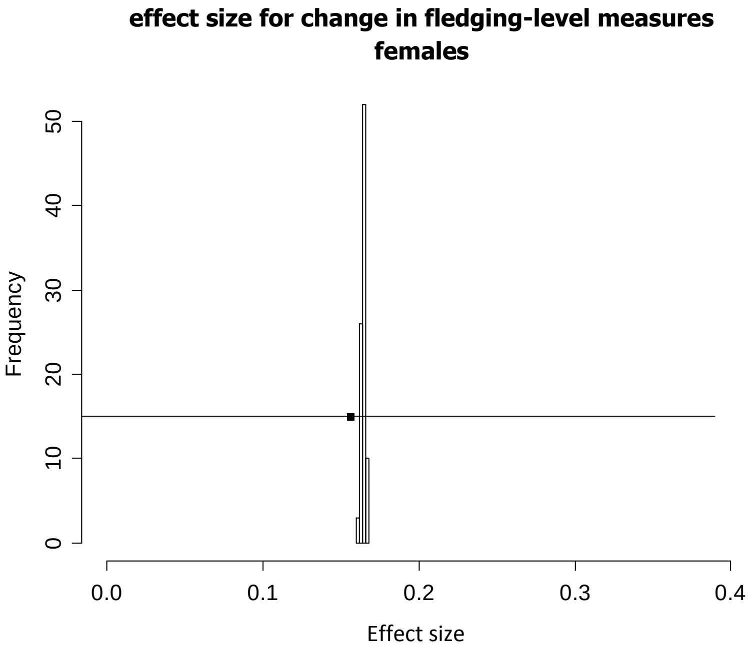

effect size for change in fledging-level measures
females
Frequency
0
10
20
30
40
50
0.0
0.1
0.2
0.3
0.4
Effect size

Figure S3. Histograms of the effect sizes (posterior mean *r* estimates) obtained for all 100 phylogenetic trees. Effect sizes were calculated for the best model of the meta-analysis on the correlation between the occurrence of divorce and change in breeding success. Squares (mean effect sizes) and error bars (95% CI) are the results of the best model run on one randomly selected tree which we present in the main article. Structure of the model: 'population' + 'phylogeny' (random effects); 'dichotomisation' + 'reference pairing class' (fixed effects). The histograms are given for the effect sizes of non-binary and non-dichotomised measures of breeding success, when divorced birds are compared to: (A) faithful birds; (B) widowed birds; (C) population mean.

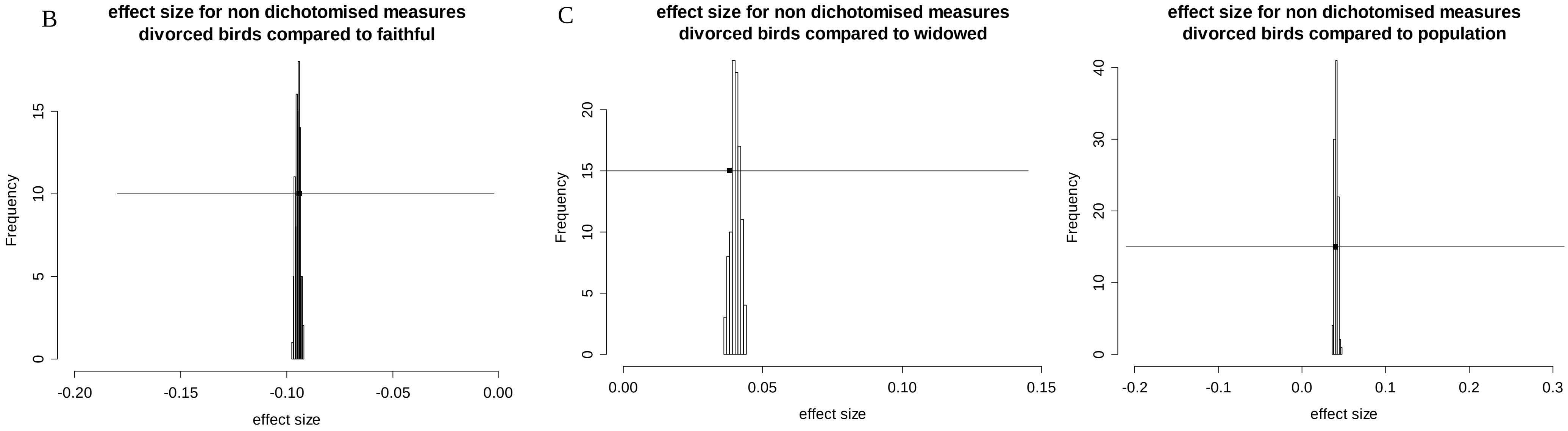


Figure S4. A forest plot of the effect size estimates *r* (squares) with 95% CI (horizontal lines) for the relationship between divorce and breeding success on the overall data set, as obtained by the random-effect model with the time when breeding success was measured (before, change, after divorce). Positive values of *r* indicate the expected relationship between breeding success and divorce if divorce was an adaptive strategy.

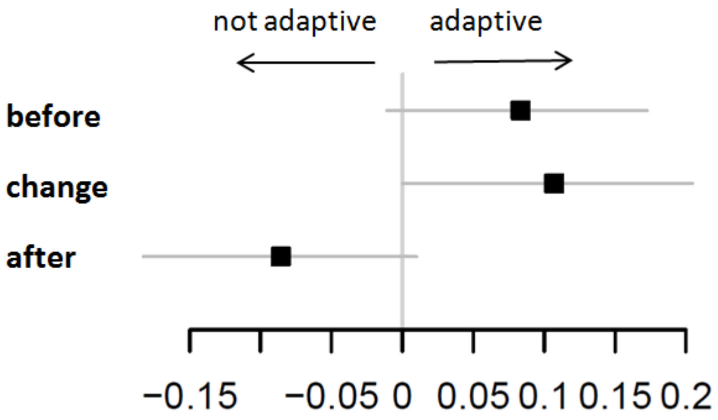


Figure S5. An example of one of the 100 phylogenetic trees of species included in the meta-analysis of the correlation between breeding success before divorce and divorce.

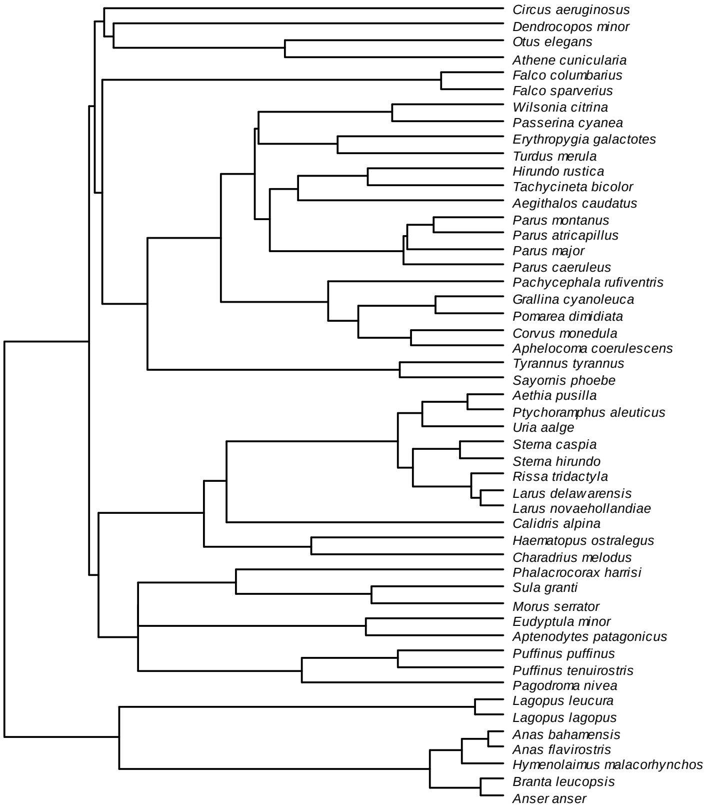


Figure S6. An example of one of the 100 phylogenetic trees of species included in the meta-analysis of the correlation between divorce and change in breeding success between the two breeding seasons.

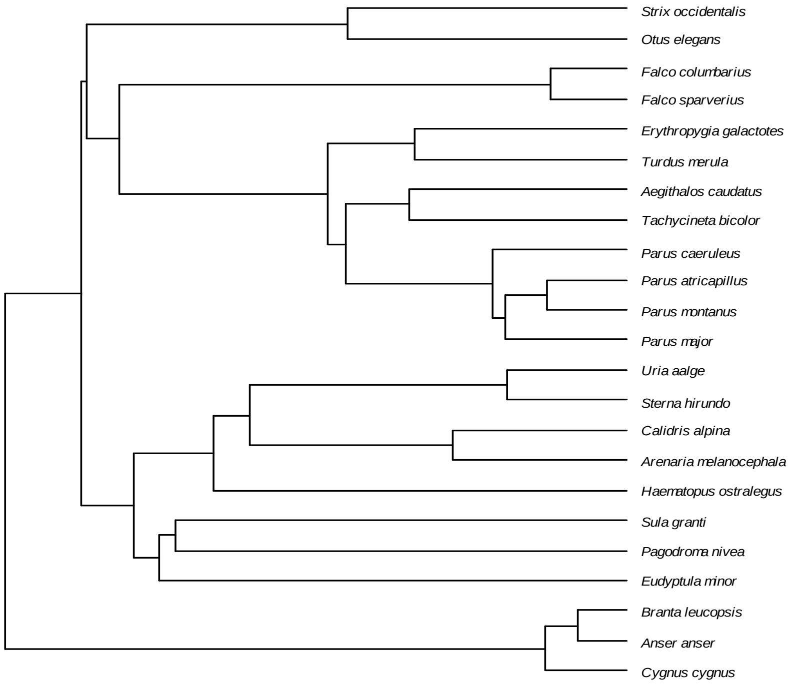


Figure S7. An example of one of the 100 phylogenetic trees of species included in the meta-analysis of the correlation between divorce and breeding success in the season after divorce.

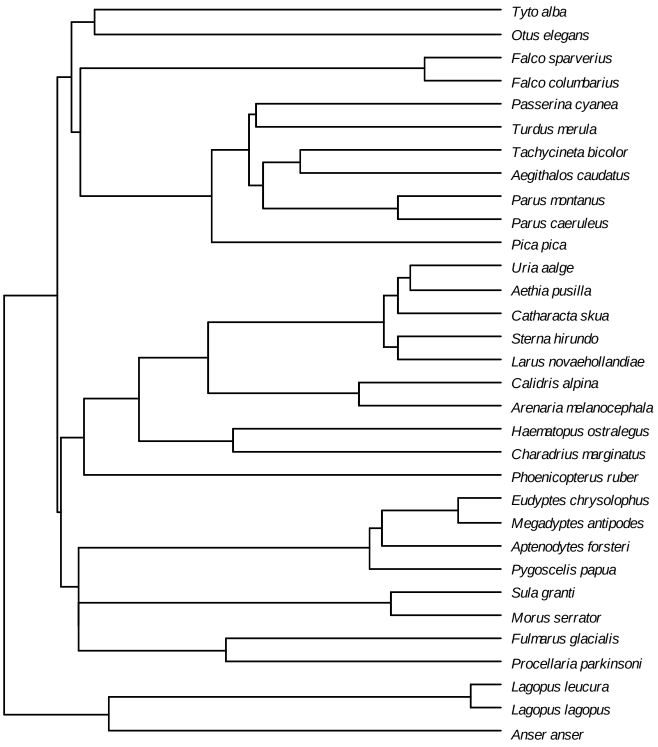


Figure S8. An example of one of the 100 phylogenetic trees of species included in the meta-analysis of the correlation between breeding success and mate change and breeding success and divorce. Species for which data only on mate change were available are marked with an asterix.

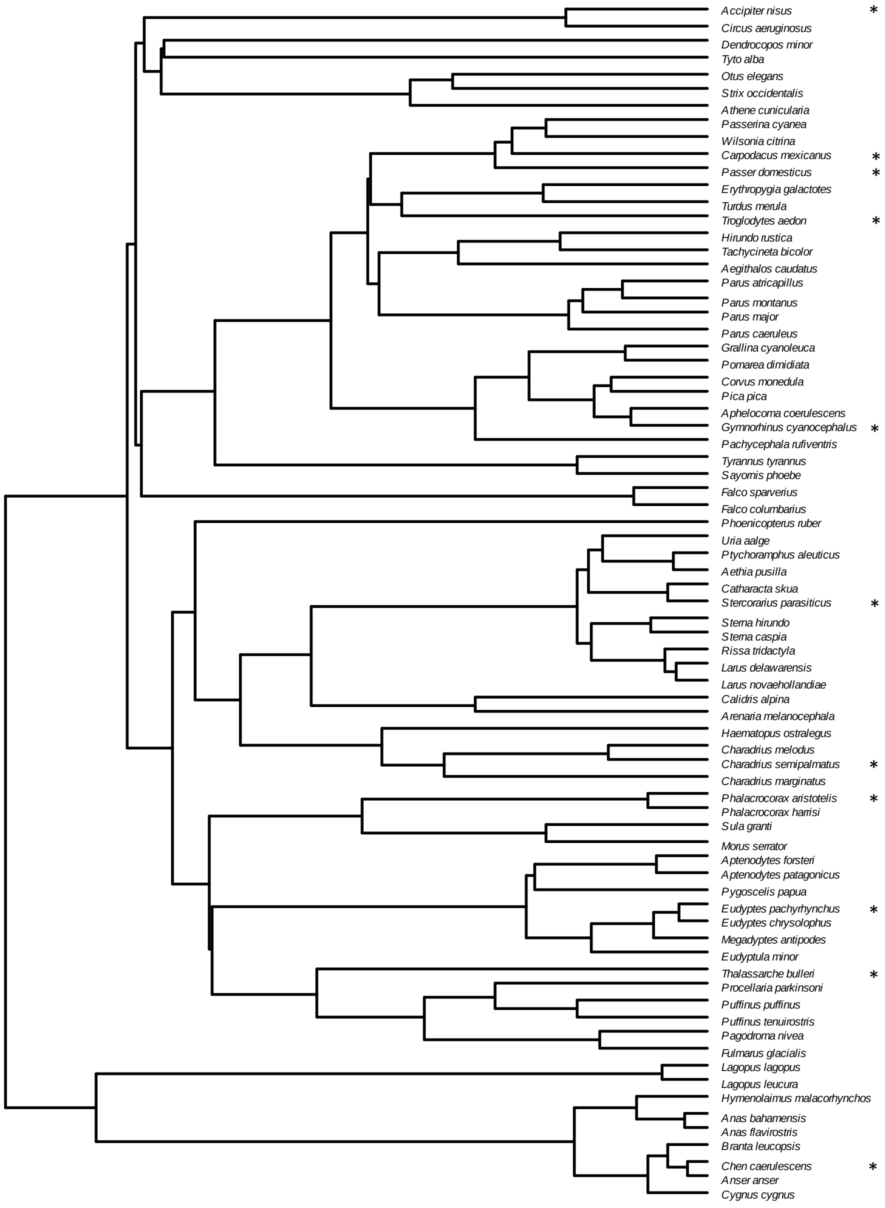


Figure S9. Funnel plots (effect sizes *versus* the standard errors of the effects) for the effect sizes of the correlation between breeding success and divorce in monogamous species on three different data sets: (A) breeding success measured before divorce; (B) breeding success expressed as a change of breeding success between the two seasons; (C) breeding success measured after divorce only. Funnel plots are constructed using all effect sizes reported in the studies (see the Section III of this appendix).

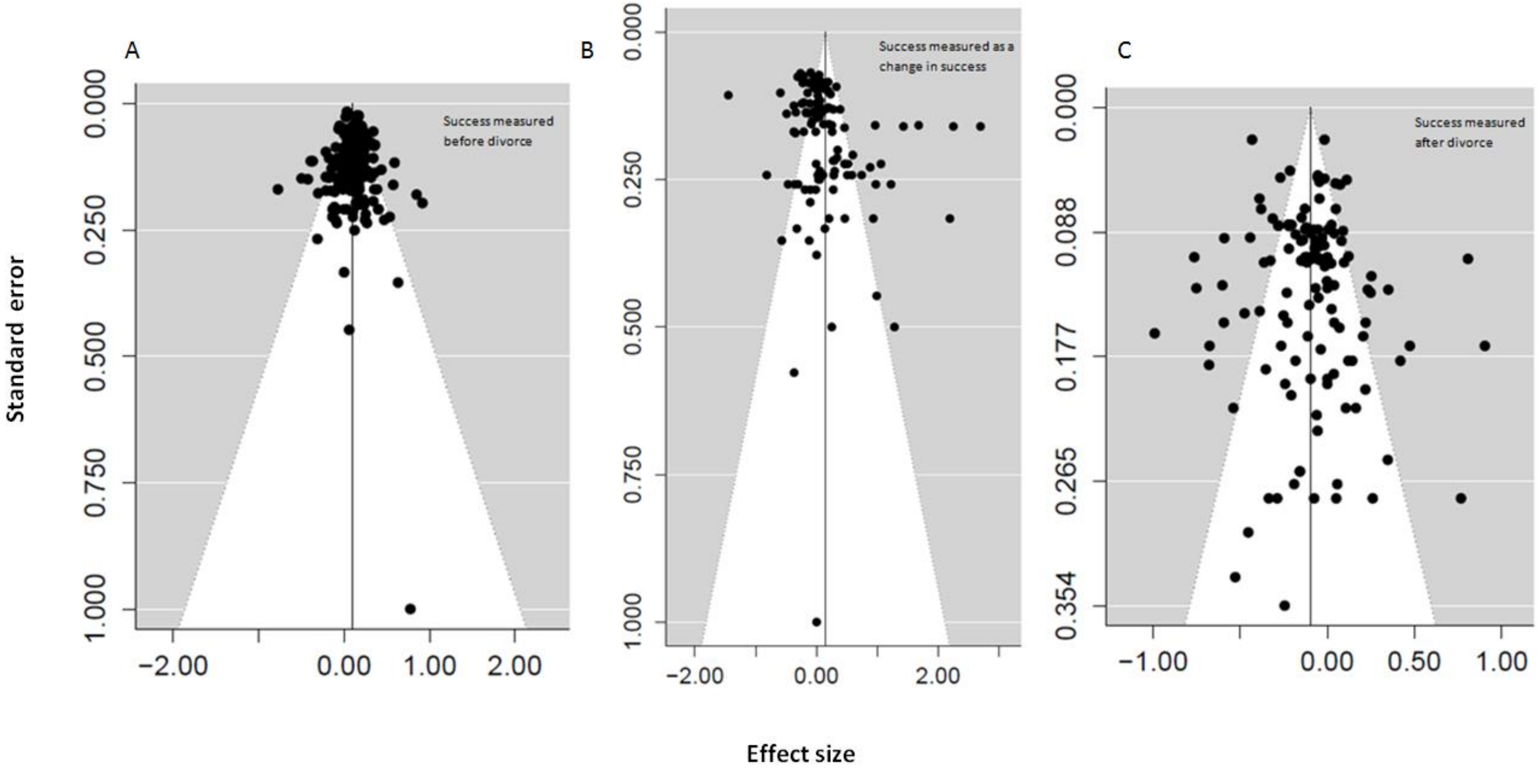


Figure S10. Histograms of the estimated number of missing studies for the 1000 trim and fill analyses performed on the data set composed of one randomly chosen effect size per study, for three meta-analyses: (A) before divorce; (B) change between the two seasons; (C) after divorce. Negative/positive values of *x* (estimated number of missing studies) indicate that the inclusion of missing data points would decrease/increase the mean effect size.

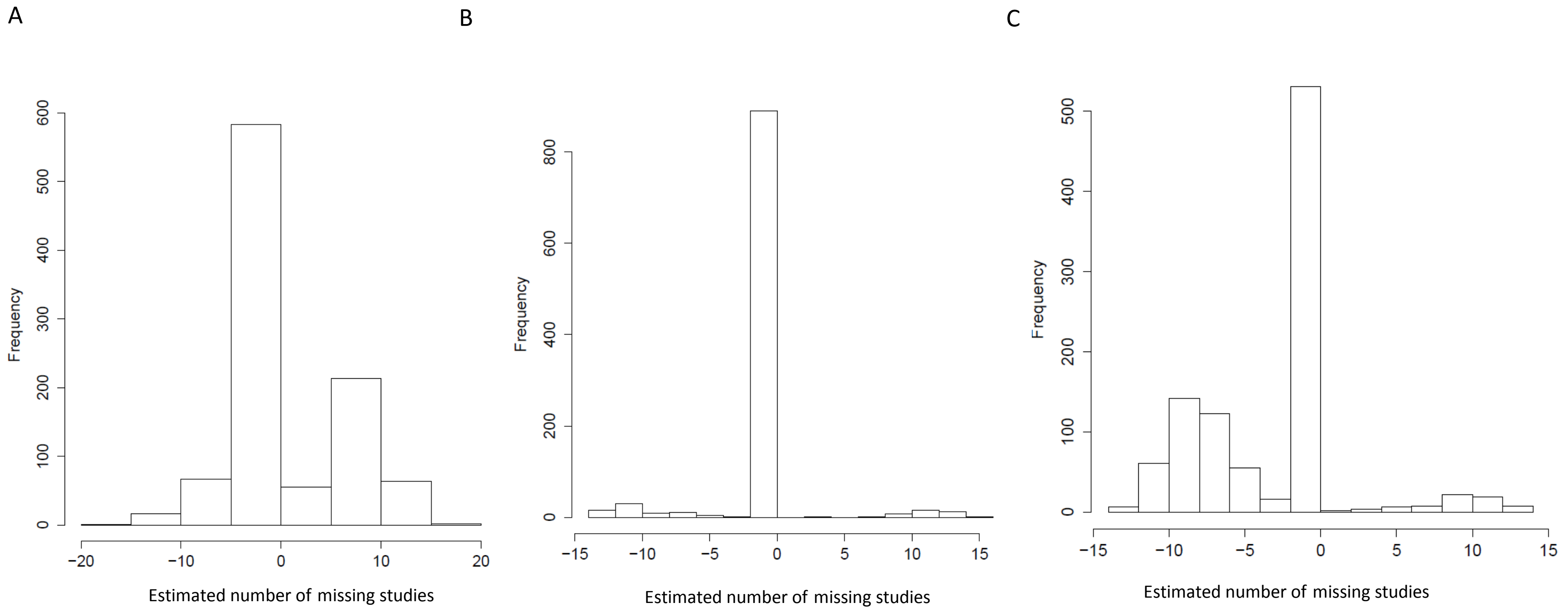


Table S3. Model summary of MCMC modelling of different random-effect structures for the relationship between breeding success and divorce in monogamous birds on the overall data set (breeding success measured before divorce, as a change in success, or after divorce). Positive values of r_{overall} correspond to the expected relationship between breeding success and divorce if divorce was adaptive. pMCMC is the *P*-value calculated in MCMCglmm for the intercept.

Random structure	DIC	r_{before} (lower/upper 95% CI)	Variation explained by random effects (%)		pMCMC
			species/phylogenetic tree	population	
–	377.79	0.058 (0.025/0.095)	–	–	0.0004
population	136.24	0.049(−0.009/0.102)	–	42.3	0.084
species	260.94	0.023 (0.020/0.066)	7.3	–	0.790
phylogenetic tree	263.34	0.006 (−0.109/0.112)	10.8	–	0.866
population + phylogenetic tree	137.09	0.032 (−0.075/0.121)	5.7	38.4	0.458

Meta-analysis on the effect size of breeding success before divorce and divorce

Table S4. Model summary of MCMC modelling of different random-effect structures for the relationship between breeding success in the season before divorce and divorce in monogamous birds. Positive values of r_{before} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Random structure	DIC	r_{before} (lower/upper 95% CI)	Variation explained by random effects (%)		pMCMC*
			species/phylogenetic tree	population	
–	−42.66	0.099 (0.069/0.131)	–	–	<1e-04
population	−625.74	0.108 (0.067/0.151)	–	95.0	<6e-06
species	−513.81	0.116 (0.063/0.16995)	91.7	–	8.89e-05
phylogenetic tree	−445.28	0.093 (−0.102/0.288)	94.2	–	0.325
population + phylogenetic tree	−625.10	0.100 (−0.022/0.213)	51.3	45.0	0.084

***** pMCMC is the p-value calculated in MCMCglmm for the intercept.

Table S5. Model summary of MCMC modelling of methodological moderators of the effect size of the relationship between breeding success before divorce and divorce in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{before} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	Effect	r_{before}	lower/upper 95% CI	pMCMC**
intercept only	−625.104		0.100	−0.022/0.209	0.0845
data quality	−636.090	intercept	0.190	0.028/0.337	0.033
		data quality	−0.033	−0.078/0.010	0.14
dichotomisation	−622.557	non-binary and non-dichotomised	0.090	−0.041/0.215	0.145
		non-binary but dichotomised	0.074	−0.053/0.196	0.200
		binary	0.195	0.029/0.354	0.022
dichotomisation x relative clutch size	−626.990	non-binary and non-dichotomised	0.095	−0.110/0.281	0.307
		non-binary but dichotomised	0.186	0.005/0.369	0.051
		binary	0.220	0.038/0.413	0.019
		clutch size	0.000	−0.029/0.020	0.9504
		non-binary but dichotomised x clutch size	−0.025	−0.055/0.004	0.093
reference pairing class*	−637.183	A	0.100	−0.012/0.208	0.077
		B	0.111	−0.01/0.223	0.067
		C	−0.110	−0.274/0.060	0.192
reference pairing class + dichotomisation	−635.706	A (non-binary and non-dichotomised)	0.090	−0.037/0.211	0.134
		B (non-binary and non-dichotomised)	0.101	−0.032/0.227	0.115
		C (non-binary and non-dichotomised)	−0.120	−0.291/0.057	0.178
		non-binary but dichotomised	−0.016	−0.071/0.041	0.586
		binary	0.105	−0.041/0.249	0.144
reference pairing	−644.203	A	0.173	0.013/0.323	0.040

class + data quality		B	0.181	0.019/0.330	0.033
		C	−0.030	−0.239/0.181	0.782
		data quality	−0.027	−0.071/0.018	0.237
dichotomisation + data quality	−631.466	non-binary and non-dichotomised	0.168	0.000/0.327	0.054
		non-binary but dichotomised	0.165	−0.015/0.329	0.071
		binary	0.279	0.078/0.459	0.008
		data quality	−0.032	−0.078/0.014	0.171
reference pairing class + dichotomisation + data quality	−641.340	intercept (A, non-binary and non-dichotomised)	0.150	−0.016/0.307	0.079
		B	0.008	−0.038/0.055	0.724
		C	−0.202	−0.325/−0.071	0.002
		non-binary but dichotomised	−0.007	−0.066/0.052	0.822
		binary	0.111	−0.035/0.256	0.125
		data quality	−0.024	−0.070/0.022	0.295
reference pairing class + dichotomisation x relative clutch size + data quality	−644.114	non-binary and non-dichotomised	0.135	−0.092/0.358	0.231
		non-binary but dichotomised	0.232	0.015/0.446	0.041
		binary	0.265	0.047/0.488	0.018
		clutch size	0.001	−0.027/0.032	0.950
		data quality	−0.019	−0.065/0.028	0.414
		B	0.008	−0.039/0.055	0.738
		C	−0.205	−0.338/−0.073	0.002
		dichotomised x clutch size	−0.024	−0.055/0.004	0.094

*reference pairing class: divorced birds are compared to faithful birds (A), to widowed birds (B), or to population mean (C).

**pMCMC is the *P*-value calculated in MCMCglmm for the intercept.

Table S6. Model summary of MCMC modelling of the effect size of the relationship between breeding success at different stages of the breeding cycle achieved before divorce and divorce in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{before} correspond to the expected relationship between breeding success and divorce if divorce was adaptive. For details on the categories that variables breeding stage 1, 2, and 3 can take, refer to Table 1 in the main article.

Fixed-effect structure of the model	DIC	Effect	r_{before}	lower/upper 95% CI	pMCMC
breeding stage + reference pairing class* + data quality	−654.980	timing (A)	0.226	0.055/0.382	0.013
		clutch size (A)	0.231	0.061/0.391	0.012
		brood (A)	0.147	−0.026/0.308	0.092
		fledging (A)	0.145	−0.025/0.305	0.093
		B	0.007	−0.040/0.052	0.779
		C	−0.200	−0.324/−0.071	0.003
		data quality	−0.019	−0.064/0.025	0.391
breeding stage 2 + reference pairing class + data quality	-643.591	timing (A)	0.226	0.063/0.387	0.012
		clutch size (A)	0.232	0.063/0.389	0.011
		hatching success (A)	0.155	−0.018/0.322	0.083
		N of hatched young (A)	0.170	−0.010/0.337	0.065
		fledging success (A)	0.165	−0.005/0.329	0.064
		N of fledglings (A)	0.138	−0.033/0.296	0.107
		B	0.007	−0.041/0.052	0.756
		C	−0.199	−0.319/−0.066	0.003
		data quality	−0.023	−0.068/0.023	0.315
breeding stage 3** + reference pairing class + data quality	−642.094	timing (A)	0.182	−0.010/0.346	0.056
		clutch size (A)	0.183	−0.010/0.352	0.058
		hatching success 1 (A)	0.161	−0.021/0.330	0.084
		hatching success 2 (A)	−0.081	−0.309/0.153	0.501
		N of hatched young 1 (A)	0.171	−0.018/0.343	0.075
		N of hatched young 2 (A)	0.071	−0.159/0.286	0.524
		fledging success 2 (A)	0.130	−0.070/0.308	0.181
		fledging success 1 (A)	0.155	−0.030/0.322	0.095

	N of fledglings 2 (A)	0.093	−0.097/0.275	0.317
	N of fledglings 1 (A)	0.108	−0.073/0.280	0.228
	B	0.008	−0.040/0.053	0.746
	C	−0.202	−0.326/−0.074	0.002
	Data quality	−0.017	−0.063/0.029	0.470

*Same notation as in Table S3.

** hatching success/ *N* of hatched young 1 = hatching success/ *N* of hatched young for all pairs laying a clutch; hatching success/ *N* of hatched young 2 = hatching success/ *N* of hatched young for pairs that hatched young; fledging success/ *N* of fledglings 1 = fledging success/ *N* of fledglings for all pairs laying a clutch; fledgling success/ *N* of fledglings 2 = fledging success/ *N* of fledglings for pairs that hatched young.

Table S7. Model summary of MCMC modelling of whether controlling for the effect of age (i.e. effect sizes obtained controlling for the age of pair members) influenced the overall effect size of the relationship between breeding success before divorce and divorce in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{before} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	Effect	r_{before}	lower/upper 95% CI	pMCMC
breeding stage + reference pairing class* + data quality	−654.980	timing (A)	0.226	0.055/0.382	0.013
		clutch size (A)	0.231	0.061/0.391	0.012
		brood (A)	0.147	−0.026/0.308	0.092
		fledging (A)	0.145	−0.025/0.305	0.093
		B	0.007	−0.040/0.052	0.779
		C	−0.200	−0.324/−0.071	0.003
		data quality	−0.019	−0.064/0.025	0.391
breeding stage + reference pairing class + data quality + controlled for age	−652.134	timing (A)	0.232	0.054/0.410	0.015
		clutch size (A)	0.238	0.061/0.421	0.014
		brood (A)	0.170	−0.010/0.337	0.065
		fledging (A)	0.165	−0.005/0.329	0.064
		B	0.007	−0.039/0.053	0.765
		C	−0.208	−0.344/−0.070	0.003
		data quality	−0.020	−0.063/0.025	0.383
		controlled for age	−0.012	−0.096/0.073	0.765
breeding stage x controlled for age + reference pairing class + data quality	−648.060	timing (A)	0.232	0.053/0.405	0.014
		clutch size (A)	0.246	0.064/0.421	0.010
		brood (A)	0.157	−0.014/0.335	0.080
		fledging (A)	0.154	−0.019/0.325	0.080
		B	0.007	−0.040/0.054	0.757
		C	−0.197	−0.342/−0.055	0.007
		data quality	−0.020	−0.065/0.024	0.371
		controlled for age	−0.061	−0.312/0.173	0.624
		timing x controlled for age	0.093	−0.178/0.372	0.506
		clutch size x controlled for age	0.053	−0.258/0.370	0.744
		fledging x controlled for age	0.017	−0.270/0.310	0.932

*Same notation as in Table S3.

Table S8. Model summary of MCMC modelling of the influence of species developmental mode (precocial, semialtricial, altricial) on the effect size of the relationship between breeding success before divorce and divorce in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{before} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	Effect	r_{before}	lower/upper 95% CI	pMCMC
breeding stage + reference pairing class* + data quality	–654.980	timing (A)	0.226	0.055/0.382	0.013
		clutch size (A)	0.231	0.061/0.391	0.012
		brood (A)	0.147	–0.026/0.308	0.092
		fledging (A)	0.145	–0.025/0.305	0.093
		B	0.007	–0.040/0.052	0.779
		C	–0.200	–0.324/–0.071	0.003
		data quality	-0.019	-0.064/0.025	0.391
breeding stage + reference pairing class + data quality + developmental mode	–653.170	timing (A, altricial)	0.227	0.042/0.413	0.020
		clutch size (A, altricial)	0.234	0.043/0.418	0.019
		brood (A, altricial)	0.144	–0.038/0.330	0.121
		fledging (A, altricial)	0.143	–0.040/0.323	0.124
		precocial	0.007	–0.138/0.153	0.920
		B	0.008	–0.039/0.054	0.744
		C	-0.202	–0.335/-0.071	0.003
		data quality	-0.019	–0.063/0.026	0.395
breeding stage x developmental mode + reference pairing class + data quality	–646.405	timing (A, altricial)	0.230	0.044/0.420	0.022
		clutch size (A)	0.224	0.034/0.414	0.027
		brood (A)	0.139	–0.050/0.324	0.142
		fledging (A)	0.138	–0.048/0.319	0.137
		B	0.007	–0.039/0.054	0.751
		C	–0.204	–0.335/–0.071	0.002
		data quality	–0.019	–0.063/0.026	0.403
		precocial	0.022	–0.167/0.219	0.818
		timing x precocial	–0.073	–0.308/0.169	0.542
		clutch size x precocial	–0.029	–0.220/0.276	0.814
		fledging x precocial	–0.020	–0.207/0.177	0.829

*Same notation as in Table S3.

Table S9. Model summary of MCMC modelling of the influence of species longevity and coloniality on the effect size of the relationship between breeding success before divorce and divorce in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{before} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	Effect	r_{before}	lower/upper 95% CI	pMCMC
coloniality + longevity + reference pairing class* + data quality	−644.945	not colonial (A)	0.048	−0.153/0.241	0.605
		loose colonies (A)	0.131	−0.094/0.352	0.244
		colonial (A)	0.023	−0.210/0.252	0.831
		longevity	0.014	0.002/0.026	0.020
		B	0.007	−0.040/0.054	0.750
		C	−0.202	−0.335/−0.072	0.003
		data quality	−0.021	−0.065/0.023	0.363
coloniality + longevity + reference pairing class + rata quality + relative clutch size	−644.597	non colonial (A)	0.109	−0.143/0.346	0.385
		loose colonies (A)	0.189	−0.073/0.427	0.151
		colonial (A)	0.073	−0.194/0.326	0.576
		longevity	0.012	−0.002/0.025	0.074
		B	0.006	−0.041/0.053	0.807
		C	−0.198	−0.319/−0.066	0.003
		data quality	−0.021	−0.0650.024	0.354
		relative clutch size	−0.009	−0.033/0.015	0.453
reference pairing class + data quality + relative clutch size	−645.851	A	0.239	0.071/0.393	0.009
		B	0.245	0.074/0.396	0.007
		C	0.044	−0.178/0.264	0.694
		data quality	−0.026	−0.069/0.019	0.251
		clutch size	−0.017	−0.036/0.002	0.078

*Same notation as in Table S3.

Table S10. Model summary of MCMC modelling of the influence of extra-pair brood rate (EP rate), divorce rate and site fidelity (weak, moderate, strong) of the species on the effect size of the relationship between breeding success before divorce and divorce in monogamous birds. All models have the same random-effect structure ('phylogenetic tree' and 'population'). Positive values of r_{before} correspond to the expected relationship between breeding success and divorce if divorce was adaptive. These models are run on three different subsets of the data for which information on EP rate, divorce, or site fidelity was available.

Fixed-effect structure of the model	DIC	Effect	r_{before}	lower/upper 95% CI	pMCMC
Extra-pair brood rate data set					
intercept only	−448.439	intercept	0.090	−0.057/0.233	0.182
EP rate	−449.433	intercept	0.088	−0.077/0.242	0.240
		EP rates	0.012	−0.349/0.383	0.969
Divorce rate data set					
intercept only	−620.111	intercept	0.096	−0.029/0.217	0.113
divorce rate	−620.217	intercept	0.096	−0.051/0.231	0.166
		divorce rate	0.009	−0.223/0.248	0.959
Site fidelity data set					
intercept only	−562.078	intercept	0.104	−0.001/0.208	0.057
site fidelity	−563.694	weak	0.051	−0.316/0.406	0.791
		moderate	0.128	−0.059/0.302	0.162
		strong	0.101	−0.015/0.210	0.078
longevity + coloniality + clutch size	−565.122	intercept	0.065	−0.161/0.278	0.547
		longevity	0.015	0.002/0.027	0.018
		colonial	−0.116	−0.279/0.057	0.176
		non-colonial	−0.057	−0.220/0.108	0.494
		clutch size	−0.001	−0.025/0.024	0.921
site fidelity + longevity + coloniality + clutch size	−563.621	weak (semi-colonial)	−0.050	−0.430/0.344	0.807
		moderate (semi-colonial)	0.120	−0.136/0.364	0.349
		strong (semi-colonial)	0.058	−0.195/0.299	0.623
		longevity	0.016	0.003/0.029	0.014
		colonial	−0.130	−0.306/0.057	0.167
		non-colonial	−0.074	−0.243/0.105	0.408
		clutch size	0.001	−0.024/0.027	0.974

Meta-analysis on the effect size of change in breeding success and divorce

Table S11. Model summary of MCMC modelling of different random-effect structures for the relationship between divorce and change in breeding success between two breeding seasons in monogamous birds. Positive values of r_{change} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Random structure	DIC	r_{change} (lower/upper 95% CI)	Variation explained by random effects (%)		pMCMC*
			species/phylogenetic tree	population	
-	208.478	0.159 (0.065/0.257)	–	–	0.001
population	85.562	0.134 (−0.045/0.310)	–	75.9	0.137
species	196.003	0.090 (−0.052/0.222)	90.0	–	0.203
phylogenetic tree	196.648	0.066 (−0.178/0.277)	14.0	–	0.486
population + phylogenetic tree	85.115	0.100 (−0.176/0.353)	10.8	67.0	0.390

***** pMCMC is the *P*-value calculated in MCMCglmm for the intercept.

Table S12. Model summary of MCMC modelling of methodological moderators of the effect size of the relationship between divorce and change in breeding success between two breeding seasons in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{change} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed effects	DIC	Effect	r_{change}	lower/upper 95% CI	pMCMC
intercept only	85.115	intercept	0.100	−0.176/ 0.353	0.390
data quality	87.830	Intercept	0.605	0.010/0.880	0.047
		data quality	−0.226	−0.442/0.007	0.063
dichotomisation	79.862	non-binary and non-dichotomised	0.256	0.018/0.467	0.041
		non-binary but dichotomised	−0.133	−0.481/0.254	0.494
		binary	−0.454	−0.778/0.050	0.073
dichotomisation	80.914	non-binary and non-dichotomised	0.224	−0.263/0.715	0.351

x relative clutch size		non-binary but dichotomised	−0.213	−0.982/0.567	0.584
		binary	−0.505	−0.977/0.054	0.081
		relative clutch size	0.006	−0.071/0.086	0.854
		dichotomised x clutch size	0.008	−0.117/0.134	0.905
reference pairing class*	90.414	A	0.175	−0.202/0.499	0.325
		B	-0.020	−0.352/0.326	0.992
		C	0.157	−0.255/0.511	0.414
		E	0.083	−0.195/0.339	0.500
reference pairing class + dichotomisation	85.577	A (non-binary and non-dichotomised)	0.287	−0.048/0.563	0.089
		B (non-binary and non-dichotomised)	0.163	−0.180/0.466	0.332
		C (non-binary and non-dichotomised)	0.250	−0.110/0.561	0.166
		E (non-binary and non-dichotomised)	0.254	−0.017/0.483	0.061
		non-binary but dichotomised	-0.368	−0.656/0.023	0.060
		binary	-0.630	−0.868/−0.156	0.014
reference pairing class + data quality	90.825	A	0.716	0.152/0.930	0.022
		B	0.563	−0.059/0.868	0.071
		C	0.713	0.100/0.931	0.028
		E	0.666	0.090/0.904	0.027
		data quality	−0.267	−0.478/-0.028	0.031
dichotomisation + data quality	81.695	non-binary and non-dichotomised	0.667	0.162/0.896	0.016
		non-binary but dichotomised	0.411	−0.285/0.825	0.241
		binary	0.084	−0.623/0.716	0.830
		data quality	−0.207	−0.415/0.019	0.076
reference pairing class + dichotomisation + data quality	85.176	intercept (A, non-binary and non-dichotomised)	0.732	0.210/0.927	0.012
		B	−0.192	−0.493/0.150	0.266
		B	−0.024	−0.250/0.207	0.839
		E	−0.049	−0.352/0.270	0.759
		non-binary but dichotomised	−0.335	−0.632/0.045	0.082
		binary	−0.603	−0.854/−0.144	0.016
		value	−0.238	−0.445/−0.002	0.047

*same notation as in Table S3; E, breeding success at *t*–1 and *t* of divorced birds compared.

Table S13. Model summary of MCMC modelling of the effect size of the relationship between divorce and change in breeding success at different stages of breeding cycle in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{change} correspond to the expected relationship between breeding success and divorce if divorce was adaptive. For details on the categories that variables breeding stage 1, 2, and 3 can take refer to Table 1 in the main article.

Fixed-effect structure of the model	DIC	Effect	Effect size	lower/upper 95% CI	pMCMC
breeding stage + dichotomy	82.953	timing (non-binary and non-dichotomised)	0.342	0.094/0.553	0.014
		clutch size (non-binary and non-dichotomised)	0.190	–0.086/0.445	0.165
		brood (non-binary and non-dichotomised)	0.360	0.046/0.606	0.028
		fledging (non-binary and non-dichotomised)	0.217	–0.024/0.436	0.075
		non-binary but dichotomised	–0.352	–0.646/0.030	0.069
		binary	–0.609	–0.854/–0.140	0.015
breeding stage 2 + dichotomisation	83.386	timing (non-binary and non-dichotomised)	0.348	0.099/0.558	0.012
		clutch (non-binary and non-dichotomised)	0.195	–0.080/0.448	0.155
		hatching success (non-binary and non-dichotomised)	0.585	0.226/0.803	0.004
		N of young hatched	0.181	–0.201/0.514	0.343
		fledging success (non-binary and non-dichotomised)	0.344	–0.051/0.646	0.085
		N of fledglings	0.210	–0.028/0.434	0.084
		non-binary but dichotomised	-0.477	–0.749/–0.069	0.023
		binary	-0.688	–0.904/–0.203	0.010
breeding stage 3* + dichotomisation	90.155	timing	0.341	0.077/0.553	0.017
		clutch size	0.186	–0.111/0.457	0.208
		hatching success 1 (non-binary and non-dichotomised)	0.595	0.160/0.833	0.011
		hatching success 2 (non-binary and non-dichotomised)	0.645	0.123/0.891	0.022
		N of young hatched 1	0.131	–0.303/0.530	0.562

	N of young hatched 2	0.261	−0.334/0.708	0.391
	fledging success 2 (non-binary and non-dichotomised)	0.290	−0.143/0.645	0.194
	fledging success 1 (non-binary and non-dichotomised)	0.488	−0.140/0.832	0.116
	N of fledglings 2	0.193	−0.106/0.460	0.191
	N of fledglings 1	0.223	−0.064/0.473	0.116
	non-binary but non-dichotomised	−0.527	−0.796/−0.064	0.023
	binary	−0.771	−0.952/−0.176	0.010

*same notation as in Table S4.

Table S14. Model summary of MCMC modelling of the level at which breeding success was measured (males, females, individuals) on the effect size of the relationship between divorce and change in breeding success in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{change} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	Effect	r_{change}	lower/upper 95% CI	pMCMC
measured for + breeding stage + dichotomisation	72.847	timing (non-binary and non-dichotomised, females)	0.361	0.096/0.576	0.015
		clutch (non-binary and non-dichotomised, females)	0.231	−0.060/0.489	0.115
		brood (non-binary and non-dichotomised, females)	0.399	0.085/0.642	0.020
		fledging (non-binary and non-dichotomised, females)	0.251	−0.008/0.476	0.060
		non-binary but dichotomised	−0.395	−0.672/−0.012	0.042
		binary	−0.693	−0.904/−0.225	0.008
		males	−0.157	−0.274/−0.038	0.012
		individuals	0.179	−0.290/0.581	0.452
measured for x breeding stage + dichotomisation	66.442	females timing	0.293	0.011/0.527	0.048
		females clutch	0.181	−0.122/0.448	0.291
		females brood	0.637	0.328/0.817	0.001
		females fledging	0.156	−0.110/0.393	0.224
		males timing	0.133	−0.187/0.421	0.389
		males clutch	0.014	−0.304/0.320	0.916
		males brood	−0.003	−0.370/0.365	1.000
		males fledging	0.102	−0.171/0.350	0.422
		individuals timing	0.756	0.309/0.931	0.005
		individuals brood	0.359	−0.313/0.791	0.286
		individuals fledging	0.222	−0.277/0.627	0.376
		non-binary but dichotomised	−0.178	−0.565/0.273	0.436
		binary	−0.598	−0.864/-0.069	0.029

Table S15. Model summary of MCMC modelling of whether controlling for the effect of age (i.e. effect sizes obtained controlling for the age of pair members) influenced the overall effect size of the relationship between divorce and change in breeding success in monogamous birds. All models have the same random-effect structure ('phylogenetic tree' + 'population'). Positive values of r_{change} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	Effect	r_{change}	lower/upper 95% CI	pMCMC
measured for x breeding stage + dichotomisation	66.442	females timing	0.293	0.011/0.527	0.048
		females clutch	0.181	−0.122/0.448	0.291
		females brood	0.637	0.328/0.817	0.001
		females fledging	0.156	−0.110/0.393	0.224
		males timing	0.133	−0.187/0.421	0.389
		males clutch	0.014	−0.304/0.320	0.916
		males brood	−0.003	−0.370/0.365	1.000
		males fledging	0.102	−0.171/0.350	0.422
		individuals timing	0.756	0.309/0.931	0.005
		individuals brood	0.359	−0.313/0.791	0.286
		individuals fledging	0.222	−0.277/0.627	0.376
		non-binary but dichotomised	−0.178	−0.565/0.273	0.436
		binary	−0.598	−0.864/-0.069	0.029
measured for x breeding stage + dichotomisation + controlled for age	69.735	females timing	0.304	−0.011/0.591	0.048
		females clutch	0.186	−0.124/0.488	0.218
		females brood	0.750	0.354/0.955	0.001
		females fledging	0.156	−0.110/0.420	0.223
		males timing	0.133	−0.187/0.421	0.389
		males clutch	0.012	−0.312/0.339	0.922
		males brood	−0.001	−0.397/0.386	0.996
		males fledging	0.102	−0.171/0.372	0.428
		individuals timing	0.994	0.298/0.931	0.005
		individuals brood	0.383	−0.327/0.791	0.282
		individuals fledging	0.234	−0.286/0.627	0.376
		non-binary but	−0.180	−0.660/0.265	0.425

		dichotomised			
		binary	–0.693	–0.864/–0.069	0.029
		controlled for age	–0.033	–0.358/0.282	0.836
measured for x breeding stage x controlled for age + dichotomisation	77.370	females timing	0.323	–0.020/0.626	0.046
		females clutch	0.180	–0.140/0.508	0.259
		females brood	0.750	0.328/0.955	0.001
		females fledging	0.162	–0.119/0.429	0.223
		males timing	0.136	–0.195/0.457	0.392
		males clutch	–0.032	–0.373/0.310	0.862
		males brood	–0.004	–0.400/0.393	0.991
		males fledging	0.102	–0.182/0.374	0.429
		individuals timing	0.994	0.305/0.931	0.005
		individuals brood	0.405	–0.344/0.791	0.287
		individuals fledging	0.258	–0.344/0.852	0.388
		non-binary and but dichotomised	–0.195	–0.678/0.297	0.421
		binary	–0.710	–0.864/–0.046	0.036
		controlled for age	0.282	–0.420/0.982	0.421
		females timing x controlled for age	–0.403	–0.996/0.339	0.283
		females clutch x controlled for age	–0.289	–0.980/0.442	0.436
		females fledging x controlled for age	–0.307	–0.976/0.420	0.404
		Individuals fledging x controlled for age	–0.402	–0.990/0.979	0.548

Table S16. Model summary of MCMC modelling of the influence of species developmental mode (precocial, semialtricial, altricial) on the effect size of the relationship between divorce and change in breeding success in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{change} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	Effect	r_{change}	lower/upper 95% CI	pMCMC
measured for x breeding stage + dichotomisation	66.442	females timing	0.293	0.011/0.527	0.048
		females clutch	0.181	−0.122/0.448	0.291
		females brood	0.637	0.328/0.817	0.001
		females fledging	0.156	−0.110/0.393	0.224
		males timing	0.133	−0.187/0.421	0.389
		males clutch	0.014	−0.304/0.320	0.916
		males brood	−0.003	−0.370/0.365	1.000
		males fledging	0.102	−0.171/0.350	0.422
		individuals timing	0.756	0.309/0.931	0.005
		individuals brood	0.359	−0.313/0.791	0.286
		individuals fledging	0.222	−0.277/0.627	0.376
		non-binary but dichotomised	−0.178	−0.565/0.273	0.436
		binary	−0.598	−0.864/−0.069	0.029
measured for x breeding stage + dichotomisation + developmental mode	66.819	altricial females timing	0.288	−0.042/0.611	0.090
		altricial females clutch	0.169	−0.175/0.501	0.289
		altricial females brood	0.733	0.287/0.955	0.005
		altricial females fledging	0.143	−0.172/0.444	0.313
		altricial males timing	0.120	−0.241/0.463	0.463
		altricial males clutch	−0.001	−0.368/0.342	0.974
		altricial males brood	−0.019	−0.439/0.390	0.940
		altricial males fledging	0.087	−0.224/0.398	0.522
		altricial individuals timing	0.981	0.301/0.931	0.006
		altricial individuals brood	0.368	−0.354/0.891	0.304
		altricial individuals fledging	0.215	−0.325/0.751	0.419

		precocial	0.047	−0.477/0.585	0.860
		non-binary but dichotomised	−0.180	−0.660/0.295	0.450
		binary	−0.693	−0.864/−0.069	0.036
measured for x breeding stage x developmental mode + dichotomisation	68.950	altricial females timing	0.265	−0.084/0.604	0.127
		altricial females clutch	0.147	−0.206/0.509	0.365
		altricial females brood	0.697	0.227/0.912	0.009
		altricial females fledging	0.123	−0.212/0.442	0.398
		altricial males timing	0.097	−0.285/0.451	0.558
		altricial males clutch	−0.023	−0.391/0.351	0.391
		altricial males brood	−0.045	−0.483/0.351	0.849
		altricial males fledging	0.049	−0.287/0.380	0.707
		altricial individuals timing	0.975	0.338/0.997	0.005
		altricial individuals brood	0.390	−0.332/0.994	0.288
		altricial individuals fledging	0.289	−0.267/0.873	0.311
		precocial	0.216	−0.883/0.811	0.732
		non-binary but dichotomised	−0.102	−0.591/0.417	0.675
		binary	−0.710	−0.915/−0.203	0.033
		precocial females fledging	−0.144	−0.879/0.908	0.832
		precocial males fledging	−0.003	−0.978/0.967	0.998
		precocial individuals fledging	−0.705	−0.942/0.950	0.425

Table S17. Model summary of MCMC modelling of the influence of species longevity and coloniality on the effect size of the relationship between divorce and change in breeding success in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{change} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	Effect	r_{change}	lower/upper 95% CI	pMCMC
coloniality + longevity + dichotomisation	80.316	non-colonial (non-binary and non-dichotomised)	0.161	−0.319/0.624	0.438
		loose colonies (non-binary and non-dichotomised)	−0.067	−0.878/0.811	0.901
		colonial (non-binary and non-dichotomised)	−0.000	−0.770/0.749	0.992
		longevity	0.025	−0.047/0.097	0.479
		non-binary but dichotomised	−0.358	−0.787/0.083	0.105
		binary	−0.917	−0.967/0.091	0.071
coloniality + longevity + dichotomisation + relative clutch size	80.410	non-colonial (non-binary and non-dichotomised)	−0.080	−0.910/0.858	0.861
		loose colonies (non-binary and non-dichotomised)	−0.295	−0.960/0.897	0.678
		colonial (non-binary and non-dichotomised)	−0.307	−0.891/0.683	0.571
		longevity	0.052	−0.048/0.154	0.297
		non-binary but dichotomised	−0.351	−0.668/0.069	0.100
		binary	−0.799	−0.978/0.020	0.054
		relative clutch size	0.033	−0.063/0.130	0.484
dichotomisation + relative clutch size	79.95	non-binary and non-dichotomised	0.211	−0.242/0.601	0.350
		non-binary but dichotomised	−0.181	−0.638/0.382	0.521
		binary	−0.468	−0.792/0.067	0.076
		relative clutch size	0.008	−0.062/0.081	0.808

Table S18. Model summary of MCMC modelling of the influence of extra-pair brood rate (EP rate), divorce rate, and site fidelity of the species on the effect size of the relationship between divorce and change in breeding success in monogamous birds. All models have the same random-effect structure ('phylogenetic tree' and 'population'). Positive values of r_{change} correspond to the expected relationship between breeding success and divorce if divorce was adaptive. These models are run on three different subsets of data for which information on the EP rate, divorce or site fidelity was available.

Fixed-effect structure of the model	DIC	Effect	r_{change}	lower/upper 95% CI	pMCMC
Extra-pair brood rate data set					
intercept only	78.317	intercept	0.151	–0.105/0.383	0.208
EP rate	78.434	intercept	0.084	–0.235/0.411	0.599
		EP rate	0.300	–0.589/0.867	0.521
Divorce rate data set					
intercept only	84.307	intercept	0.090	–0.193/0.344	0.446
divorce rate	84.132	intercept	0.080	–0.318/0.447	0.666
		divorce rate	0.028	–0.761/0.782	0.964
Site fidelity data set					
intercept only	86.055	intercept	0.126	–0.153/0.385	0.319
site fidelity		moderate	–0.127	–0.682/0.537	0.731
		strong	0.156	–0.142/0.418	0.246
longevity + coloniality + clutch size	85.248	intercept	–0.284	–0.938/0.803	0.678
		longevity	–0.010	–0.091/0.068	0.804
		colonial	0.188	–0.765/0.888	0.749
		non-colonial	0.479	–0.511/0.927	0.346
		clutch size	0.016	–0.095/0.124	0.767
site fidelity + longevity + coloniality + clutch size	85.210	moderate (semi-colonial)	–0.500	–0.966/0.725	0.451
		strong (semi-colonial)	–0.025	–0.911/0.887	0.971
		longevity	–0.026	–0.110/0.057	0.528
		colonial	0.197	–0.774/0.879	0.738
		non-colonial	0.538	–0.469/0.935	0.278
		clutch size	–0.014	–0.133/0.103	0.795

Meta-analysis on the effect size of divorce and breeding success in the season after divorce

Table S19. Model summary of MCMC modelling of different random-effect structures for the relationship between divorce and breeding success in the breeding season after divorce in monogamous birds. Positive values of r_{after} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Random structure	DIC	r_{after} (lower/upper 95% CI)	Variation explained by random effects (%)		pMCMC*
			species/phylogenetic tree	population	
-	41.56	−0.094 (−0.141/−0.045)	–	–	0.0002
population	13.703	−0.100 (−0.151/−0.047)	–	9.3	0.000
species	15.803	−0.104 (−0.158/−0.051)	7.6	–	2e-04
phylogenetic tree	14.592	−0.108 (−0.188/−0.033)	9.4	–	0.007
population + phylogenetic tree	12.165	−0.110 (−0.191/−0.031)	9.0	8.1	0.009

***** pMCMC is the *P*-value calculated in MCMCglmm for the intercept.

Table S20. Model summary of MCMC modelling of methodological moderators of the effect size of the relationship between divorce and breeding success in the breeding season after divorce in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{after} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	Effect	r_{after}	lower/upper 95% CI	pMCMC
intercept only	12.165	intercept	−0.110	−0.191/ −0.031	0.009
data quality	13.542	intercept	−0.100	−0.316/0.135	0.383
		data quality	−0.004	−0.091/0.083	0.948
dichotomisation	−3.716	non-binary and non-dichotomised	−0.062	−0.145/0.024	0.141
		non-binary but dichotomised	0.024	−0.092/0.143	0.684
		binary	−0.267	−0.365/−0.168	<1e-05
dichotomisation x relative clutch size	1.299	non-binary and non-dichotomised	−0.042	−0.205/0.121	0.589
		non-binary but dichotomised	0.001	−0.239/0.238	0.994
		binary	−0.328	−0.545/−0.114	0.002
		clutch size	0.008	−0.035/0.049	0.714
		non-binary but dichotomised x relative clutch size	0.032	−0.071/0.135	0.543
reference pairing class*	10.469	A	−0.134	−0.226/−0.044	0.006
		B	−0.035	−0.155/0.089	0.546
		C	−0.157	−0.425/0.137	0.285
reference pairing class + dichotomisation	−7.412	A (non-binary and non-dichotomised)	−0.094	−0.184/-0.002	0.043
		B (non-binary and non-dichotomised)	0.038	−0.082/0.158	0.530
		C (non-binary and non-dichotomised)	0.042	−0.234/0.313	0.765
		non-binary but dichotomised	0.096	−0.027/0.217	0.126
		binary	−0.238	−0.354/−0.118	3e-04
reference pairing class +	−2.830	non-binary and non-dichotomised	−0.115	−0.290/0.056	0.190
		non-binary but	−0.051	−0.292/0.186	0.664

dichotomisation x relative clutch size		dichotomised			
		binary	−0.320	−0.538/−0.103	0.003
		clutch size	0.003	−0.024/0.030	0.783
		B	0.143	0.029/0.262	0.016
		C	0.144	−0.134/0.426	0.304
		non-binary but dichotomised x relative clutch size	0.006	−0.036/0.048	0.757
		binary x relative clutch size	−0.016	−0.127/0.092	0.763
dichotomisation + data quality	11.409	non-binary and non-dichotomised	0.005	−0.211/0.227	0.962
		non-binary but dichotomised	0.091	−0.143/0.315	0.443
		binary	−0.210	−0.406/−0.001	0.049
		data quality	−0.026	−0.103/0.054	0.518
reference pairing class + data quality	−2.312	A	−0.089	−0.336/0.174	0.492
		B	0.013	−0.259/0.294	0.943
		C	−0.133	−0.431/0.196	0.407
		data quality	−0.018	−0.115/0.077	0.721
reference pairing class + dichotomisation + data quality	−5.953	intercept	−0.033	−0.266/0.207	0.786
		B	0.133	0.024/0.236	0.015
		C	0.105	−0.191/0.383	0.478
		non-binary but dichotomised	0.096	−0.031/0.219	0.135
		binary	−0.241	−0.357/−0.119	2e-4
		data quality	−0.024	−0.108/0.063	0.590

*same notation as in Table S3.

Table S21. Model summary of MCMC modelling of the effect size of the relationship between divorce and breeding success at different stages of the breeding cycle in the breeding season after divorce in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ and ‘population’). Positive values of r_{after} correspond to the expected relationship between breeding success and divorce if divorce was adaptive. For details on the categories variables breeding stage 1, 2, and 3 can take refer to Table 1 in the main article.

Fixed-effect structure of the model	DIC	Effect	r_{after}	lower/upper 95% CI	pMCMC
breeding stage + dichotomisation + reference pairing class	−6.590	timing (A)	−0.292	−0.483/−0.076	0.009
		clutch size (binary, A)	−0.317	−0.499/−0.110	0.003
		brood (binary, A)	−0.154	−0.369/0.076	0.186
		fledging (binary, A)	−0.337	−0.484/−0.170	1e-4
		skipped breeding (A)	−0.336	−0.464/−0.201	4e-5
		non-binary and non-dichotomised	0.224	−0.032/0.400	0.020
		non-binary but dichotomised	0.284	0.085/0.460	0.005
		B	0.145	0.038/0.253	0.009
		C	0.152	−0.136/0.415	0.292
breeding stage 2 + dichotomisation + reference pairing class	−3.294	timing (non-binary and non-dichotomised, A)	−0.073	−0.203/0.063	0.281
		clutch size (non-binary and non-dichotomised, A)	−0.102	−0.230/0.027	0.122
		hatching success (non-binary and non-dichotomised, A)	0.035	−0.246/0.316	0.808
		N of young hatched (non-binary and non-dichotomised, A)	0.227	−0.269/0.635	0.372
		fledging success (non-binary and non-dichotomised, A)	−0.148	−0.448/0.179	0.372
		N of fledglings (non-binary and non-dichotomised, A)	−0.124	−0.240/−0.006	0.040
		skipped breeding (non-binary and non-dichotomised, A)	−0.149	−0.484/0.239	0.438
		non-binary but dichotomised	0.092	−0.208/0.369	0.543
		binary	−0.197	−0.504/0.158	0.271
		B	0.147	0.037/0.254	0.009
		C	0.152	−0.140/0.417	0.298

breeding stage 3* + dichotomisation + reference pairing class	1.146	timing (non-binary and non-dichotomised, A)	−0.072	−0.207/0.067	0.298
		clutch size (non-binary and non-dichotomised, A)	−0.091	−0.222/0.047	0.185
		hatching success 1 (non-binary and non-dichotomised, A)	0.210	−0.270/0.611	0.394
		hatching success 2 (non-binary and non-dichotomised, A)	−0.054	−0.395/0.298	0.768
		N of young hatched 1 (non-binary and non-dichotomised, A)	0.227	−0.277/0.638	0.383
		fledging success 2 (non-binary and non-dichotomised, A)	0.003	−0.541/0.543	0.992
		fledging success 1 (non-binary and non-dichotomised, A)	−0.001	−0.440/0.446	0.994
		N of fledglings 2 (non-binary and non-dichotomised, A)	−0.116	−0.272/0.048	0.159
		N of fledglings 1 (non-binary and non-dichotomised, A)	−0.131	−0.279/0.027	0.096
		skipped breeding (non-binary and non-dichotomised, A)	0.004	−0.482/0.480	0.992
		non-binary but dichotomised	−0.056	−0.462/0.384	0.809
		binary	−0.340	−0.691/0.152	0.164
		B	0.145	0.032/0.253	0.011
		C	0.152	−0.141/0.428	0.308

*same notation as in Table S4.

Table S22. Model summary of MCMC modelling of (*a*) whether controlling for the effect of age (i.e. effect sizes obtained controlling for the age of pair members) influenced the overall effect size of the relationship between divorce and breeding success in the breeding season after divorce; and (*b*) the influence of species developmental mode (precocial, semialtricial, altricial) on the effect size in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{after} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	Effect	r_{after}	lower/upper 95% CI	pMCMC
reference pairing class* + dichotomisation	−7.412	A (non-binary and non-dichotomised)	−0.094	−0.184/−0.002	0.043
		B (non-binary and non-dichotomised)	0.038	−0.082/0.158	0.530
		C (non-binary and non-dichotomised)	0.042	−0.234/0.313	0.765
		non-binary but dichotomised	0.096	−0.027/0.217	0.126
		binary	−0.238	−0.354/−0.118	3e-04
reference pairing class + dichotomisation + controlled for age	−5.189	A (non-binary and non-dichotomised)	−0.095	−0.197/0.009	0.067
		B (non-binary and non-dichotomised)	0.039	−0.086/0.169	0.531
		C (non-binary and non-dichotomised)	0.042	−0.247/0.323	0.766
		non-binary but dichotomised	0.096	−0.025/0.227	0.130
		binary	−0.247	−0.378/−0.120	2e-4
		controlled for age	0.008	−0.212/0.230	0.948
reference pairing class + dichotomisation + developmental mode	−4.998	A (altricial, non-binary and non-dichotomised)	−0.087	−0.194/0.015	0.091
		B (altricial, non-binary and non-dichotomised)	0.044	−0.082/0.173	0.486
		C (altricial, non-binary and non-dichotomised)	0.044	−0.237/0.323	0.755
		non-binary but dichotomised	0.096	−0.030/0.221	0.131
		binary	−0.247	−0.375/−0.120	2e-4
		precocial	−0.017	−0.14612/0.1	0.789

*same notation as in Table S3.

Table S23. Model summary of MCMC modelling of the level breeding success was measured at (males, females, individuals) on the effect size of the relationship between divorce and breeding success in the breeding season after divorce in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{after} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	effect	r_{after}	lower/upper 95% CI	pMCMC
measured for + breeding stage + dichotomisation + reference pairing class*	−2.644	females (brood, A)	0.067	−0.131/0.257	0.505
		males (brood, A)	0.072	−0.127/0.268	0.481
		individuals (brood, A)	0.010	−0.255/0.268	0.944
		timing	−0.136	−0.336/0.080	0.209
		clutch	−0.166	−0.357/0.029	0.098
		fledging	−0.187	−0.352/−0.010	0.038
		skipped breeding	−0.223	−0.464/0.059	0.113
		non-binary but dichotomised	0.074	−0.072/0.217	0.319
		binary	−0.182	−0.395/0.056	0.121
		B	0.145	0.033/0.250	0.010
		C	0.144	−0.148/0.409	0.322
measured for x breeding stage + dichotomisation + reference pairing class	3.500	females timing	−0.077	−0.246/0.089	0.364
		females clutch	−0.117	−0.270/0.044	0.148
		females brood	0.006	−0.225/0.234	0.963
		females fledging	−0.124	−0.254/0.011	0.070
		females skipped breeding	−0.240	−0.519/0.085	0.147
		individuals brood	0.343	−0.190/0.732	0.209
		individuals fledging	−0.330	−0.534/−0.078	0.010
		individuals skipped breeding	−0.124	−0.505/0.304	0.567
		individuals timing	−0.040	−0.371/0.304	0.823
		males brood	−0.029	−0.302/0.247	0.834
		males clutch	−0.093	−0.254/0.076	0.271
		males fledging	−0.097	−0.233/0.042	0.169
		males skipped breeding	−0.259	−0.543/0.063	0.122

	males timing	−0.088	−0.266/0.095	0.342
	non-binary but dichotomised	0.119	−0.033/0.265	0.120
	binary	−0.116	−0.369/0.153	0.390
	B	0.160	0.052/0.269	0.004
	C	0.187	−0.101/0.448	0.198

*same notation as in Table S3.

Table S24. Model summary of MCMC modelling of the influence of species longevity and coloniality on the effect size of the relationship between divorce and breeding success in the breeding season after divorce in monogamous birds. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). Positive values of r_{after} correspond to the expected relationship between breeding success and divorce if divorce was adaptive.

Fixed-effect structure of the model	DIC	effect	r_{after}	lower/upper 95% CI	pMCMC
coloniality + longevity + dichotomisation + reference pairing class*	-3.483	non-colonial (non-binary and non-dichotomised)	−0.115	−0.236/0.004	0.052
		loose colonies non-binary and non-dichotomised)	−0.163	−0.362/0.058	0.139
		colonial (non-binary and non-dichotomised)	−0.123	−0.263/0.020	0.090
		longevity	0.004	−0.005/0.014	0.372
		non-binary but dichotomised	0.102	−0.024/0.231	0.118
		binary	−0.268	−0.417/−0.101	0.002
		B	0.143	0.030/0.252	0.013
		C	0.172	−0.143/0.454	0.272
coloniality + longevity + dichotomisation + reference pairing class + relative clutch size	−2.425	non-colonial (non-binary and non-dichotomised)	−0.179	−0.382/0.046	0.109
		loose colonies (non-binary and non-dichotomised)	−0.204	−0.430/0.051	0.111
		colonial (non-binary and non-dichotomised)	−0.160	−0.336/0.021	0.085
		longevity	0.005	−0.005/0.015	0.284
		non-binary but dichotomised	0.105	−0.025/0.231	0.110
		binary	−0.262	−0.414/−0.093	0.002
		B	0.149	0.035/0.258	0.010
		C	0.178	−0.138/0.459	0.260
		relative clutch size	0.009	−0.018/0.037	0.496
dichotomisation + reference	−4.760	non-binary and non-dichotomised	−0.116	−0.260/0.031	0.122
		non-binary but dichotomised	−0.020	−0.186/0.148	0.802

pairing class + relative clutch size	binary	−0.335	−0.450/−0.213	<6e-06
	B	0.135	0.028/0.241	0.014
	C	0.137	−0.135/0.391	0.317
	relative clutch size	0.004	−0.018/0.026	0.688

*same notation as in Table S3.

Table S25. Model summary of MCMC modelling of the influence of extra-pair brood rate (EP rate) and divorce rate on the effect size of the relationship between divorce and breeding success in the breeding season after divorce in monogamous birds. Positive values of r_{after} correspond to the expected relationship between breeding success and divorce if divorce was adaptive. All models have the same random-effect structure (‘phylogenetic tree’ + ‘population’). These models are run on three different subsets of data for which information on the EP rate or divorce was available.

Fixed-effect structure of the model	DIC	Effect	r_{after}	lower/upper 95% CI	pMCMC
Extra-pair brood rate data set					
intercept only	13.614	intercept	−0.082	−0.177/0.011	0.074
EP rate	14.912	intercept	−0.092	−0.204/0.026	0.114
		EP rate	0.048	−0.311/0.395	0.782
Divorce rate data set					
intercept only	13.354	intercept	−0.104	−0.181/−0.027	0.011
divorce rate	13.486	intercept	−0.147	−0.251/−0.043	0.008
		divorce rate	0.157	−0.111/0.408	0.245
Site fidelity data set					
intercept only	22.783	intercept	−0.106	−0.190/−0.021	0.013
site fidelity	25.475	weak	−0.200	−0.457/0.259	0.591
		medium	−0.110	−0.372/0.149	0.400
		strong	−0.080	−0.255/0.280	0.930
longevity + coloniality + clutch size	24.480	intercept	−0.188	−0.413/0.039	0.102
		longevity	−0.004	−0.013/0.005	0.388
		colonial	0.064	−0.140/0.264	0.526
		non-colonial	0.077	−0.139/0.298	0.484
		clutch size	0.012	−0.018/0.042	0.437
site fidelity + longevity + coloniality + clutch size	27.93	weak (semi-colonial)	−0.203	−0.258/0.320	0.132
		medium (semi-colonial)	−0.204	−0.549/0.149	0.241
		strong (semi-colonial)	−0.170	−0.257/0.321	0.133
		longevity	−0.004	−0.014/0.005	0.388
		colonial	0.055	−0.159/0.272	0.609
		non-colonial	0.072	−0.174/0.316	0.553
		clutch size	0.011	−0.022/0.043	0.506

Table S26. Model summary of MCMC modelling for the relationship between divorce/partner change and breeding success. All models have the same random-effect structure ('phylogenetic tree' + 'population'). Positive values of *r* correspond to the expected relationship between breeding success and divorce/partner change if divorce/partner change was adaptive.

Fixed-effect structure of the model	DIC	Effect	*r*	lower/upper 95%CI	pMCMC
(intercept only)	151.841	intercept	−0.006	−0.084/0.067	0.888
type of partner change	143.743	divorce	0.027	−0.046/0.100	0.431
		partner change	−0.074	−0.156/0.007	0.071
type of partner change + temporal contrast	81.016	divorce (after)	−0.109	−0.183/−0.032	0.006
		partner change (after)	−0.124	−0.198/−0.046	0.003
		before	0.199	0.144/0.252	< 6e-06
		change	0.198	0.129/0.263	< 6e-06
		overall	−0.128	−0.401/0.166	0.393

Table S27. Results of the trim and fill analysis on the three data sets used in three meta-analyses on the correlation between breeding success and divorce. The left-hand part of the table gives the estimated number of missing studies with the estimated mean effect size if the missing studies were included. The right-hand side of the table gives the median number of the estimated number of missing studies (with the average means of the estimated effect size) for 1000 repeated trim and fill analyses when only one randomly chosen effect size was included per study (see Section III of this appendix).

Data set	**All the effect sizes included**			**Randomly chosen one effect size/study; 1000 repeats**		
	Estimated number of missing studies	Estimated mean effect size	95% CI (lower/upper)	Median of the estimated number of missing studies	Average of the means of the estimated effect size	S.D. of the average
Before	15	0.124	0.097/0.152	0	0.102	0.024
Change	0	0.146	0.054/0.236	0	0.140	0.103
After	23	–0.170	–0.219/–0.055	0	–0.120	0.062

CHAPTER 3

A multievent approach to estimating pair fidelity and heterogeneity in state transitions

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A multievent approach to estimating pair fidelity and heterogeneity in state transitions

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Abstract

Fidelity rates of pair-bonded individuals are of considerable interest to behavioral and population biologists as they can influence population structure, mating rates, population productivity, and gene flow. Estimates of fidelity rates calculated from direct observations of pairs in consecutive breeding seasons may be biased because (i) individuals that are not seen are assumed to be dead, (ii) variation in the detectability of individuals is ignored, and (iii) pair status must be known with certainty. This can lead to a high proportion of observations being ignored. This approach also restricts the way variation in fidelity rates for different types of individuals, or the covariation between fidelity and other vital rates (e.g., survival) can be analyzed. In this study, we develop a probabilistic multievent capture–mark–recapture (MECMR) modeling framework for estimating pair fidelity rates that accounts for imperfect detection rates and capture heterogeneity, explicitly incorporates uncertainty in the assessment of pair status, and allows estimates of state-dependent survival and fidelity rates to be obtained simultaneously. We demonstrate the utility of our approach for investigating patterns of fidelity in pair-bonded individuals, by applying it to 30 years of breeding data from a wild population of great tits *Parus major* Linnaeus. Results of model selection supported state-dependent recapture, survival, and fidelity rates. Recapture rates were higher for individuals breeding with their previous partner than for those breeding with a different partner. Faithful birds that were breeding with the same partner as in the previous breeding season (i.e., at $t-1$) experienced substantially higher survival rates (between t and $t+1$) and were also more likely to remain faithful to their current partner (i.e., to remain in the faithful state at $t+1$). First year breeders were more likely to change partner than older birds. These findings imply that traditional estimates, which do not account for state-dependent parameters, may be both inaccurate and biased, and hence, inferences based on them may conceal important biological effects. This was demonstrated in the analysis of simulated capture histories, which showed that our MECMR model was able to estimate state-dependant survival and pair fidelity rates in the face of varying state-dependant recapture rates robustly, and more accurately, than the traditional method. In addition, this new modeling approach provides a statistically rigorous framework for testing hypothesis about the causes and consequences of fidelity to a partner for natural populations. The novel modeling approach described here can readily be applied, either in its current form or via extension, to other populations and other types of dyadic interactions (e.g., between nonpaired individuals, such as parent–offspring relationships, or between individuals and locations, such as nest-site fidelity).

Introduction

The pair bonds formed between males and females for the purpose of reproduction are among the most widely studied types of associations between two individuals. In birds, a group where more than 85% of species are socially monogamous (Bennett and Owens 2002), the degree to which pair bonds are maintained over consecutive breeding seasons (i.e., the pair fidelity rate) is known to be highly variable both within and between species (Black 1996). Explaining why these differences occur is important for understanding the evolution of social monogamy and long-term partnerships (reviewed in Black 1996; Reichard and Boesch 2003; Shuster and Wade 2003). Moreover, the dynamics of the formation and maintenance of pair bonds can influence population productivity and hence shape population dynamics, both through determining the number of reproductive pairs (Sugg et al. 1996; Berec and Boukal 2004; Maxin and Berec 2010), and through differences in reproductive success of newly formed and existing pairs (e.g., Pampus et al. 2005; Hatch and Westneat 2008).

Despite the importance of understanding the dynamics of pair bonds, obtaining accurate estimates of pair fidelity in wild populations remains a significant challenge. Existing estimates have been obtained from observations of marked individuals that are recaptured (or resighted) in consecutive breeding seasons (e.g., Rogers and Knight 2006; Hatch and Westneat 2008). The principal drawback of this approach is that low recapture rates (a common problem for many taxa, see in Archaux et al. 2012) can bias estimates of fidelity because a proportion of the marked individuals that are alive will not be recaptured at a particular sampling occasion. Moreover, recapture probabilities may differ among different classes of individuals because of underlying biological, ecological, or behavioral characteristics (e.g., males and females, paired and unpaired individuals; Crespin et al. 2008; Carter et al. 2012 and references therein). When such differences in detectability are ignored, biologically important effects that operate on the trait of interest may be concealed due to biases in rate estimates, and inferences based on observed patterns will be artifacts of individual encounter rates (Cubaynes et al. 2010; Carter et al. 2012; Fletcher et al. 2012).

An additional, and interrelated, problem in estimating pair fidelity rates from field observations is the inherent difficulty associated with assigning pair status with certainty. Determining whether a focal individual has been faithful to its partner from the previous season requires that both its current and previous partners are known and captured. For this to occur a large proportion of the population must be marked, and recapture rates for marked individuals must be high. As discussed above, this requirement is rarely met in studies of wild populations, and consequently, most estimates of pair fidelity rates are obtained after a substantial part of the data has been discarded (i.e., Forslund and Larsson 1991; Warkentin et al. 1991; Llambias et al. 2008).

The estimation of association rates in other types of dyadic interactions (such as associations between individuals in social network, Croft et al. 2008), where the nature or strength of association is determined from field-based observations of marked individuals could also suffer from these same problems (e.g., Voelkl et al. 2011). Therefore, if we want to robustly quantify rates of maintenance of pair bonds and other types of dyadic interactions, a modeling framework that incorporates and accounts for both imperfect and heterogeneous recapture rates, and problems connected with state assignment is needed. Such a framework would not only provide a robust method for estimating rates but would, at the same time, allow greater flexibility to test hypotheses on causes, and fitness costs and benefits of maintenance of pair bonds (e.g., the survival consequences of fidelity and mate change; see below).

Multistate capture–mark–recapture (MSCMR) is a modeling framework widely used to estimate state-dependent demographic rates (commonly survival rates) along with transition rates of individuals among different "states" (e.g., physical locations, infection status, reproductive status; Nichols et al. 1994; Lebreton and Pradel 2002), while explicitly accounting for imperfect and heterogeneous detectability of marked individuals (Arnason 1972, 1973; Hestbeck et al. 1991). As it is possible to assign individuals to different states based on their pair status (with the same partner or not), multistate models provide a framework for estimating pair fidelity rates and survival probabilities simultaneously in the same model. Moreover, by allowing different constraints to be imposed on state-dependent survival and transition parameters, these models provide a rigorous method of evaluating the fitness consequences of pair fidelity. One drawback of MSCMR models that limits their utility is that they assume there is no error or ambiguity in state assignment, an assumption rarely met in studies of pair fidelity (or other types of dyadic interactions). Recently developed multievent capture–mark–recapture models (MECMR) (Pradel 2005), however, provide an extension of the MSCMR models that explicitly accounts for unknown or partially observable states by treating them as a hidden Markov process (Pradel 2005; Rouan 2007). In MECMR models, observations of captured individuals, and indirect information from individuals that are not captured (globally termed "events"), are related to the true but unknown (hidden) state of the individual through a series of conditional probabilities (Pradel et al. 2008; Choquet et al. 2009b). Accordingly, MECMR models offer an ideal framework to obtain robust estimates of pair fidelity when there is ambiguity of state assessment.

In this paper, we present a flexible MECMR modeling framework to obtain robust estimates of pair fidelity in wild populations. We based the conceptual development of our modeling approach on the pair bond between the members of monogamous breeding pairs (where females and males exclusively associate together at the breeding site) because this is one of the most studied dyadic interactions in behavioral, population, and evolutionary ecology. Also, the way that data on pair memberships is collected is similar to the way in which information on other dyadic associations in wild are obtained.

To demonstrate the utility of our approach, we apply it to 30 years of data from a wild population of socially monogamous great tits *Parus major* Linnaeus, to estimate annual survival and fidelity rates and investigate patterns of pair fidelity in the population. We demonstrate the utility and advantages of our new modeling approach by combining the results of MECMR modeling with model selection to test the following three hypotheses: (a) pair fidelity confers benefits to individuals in terms of enhanced survival (e.g., because greater familiarity and better coordination between partners affords paired individuals an enhanced physical condition [Hall 1999; Black et al. 2007; Naves et al. 2007], while when survival is related to social rank in winter flocks, such as occurs in the great tit, one sex will benefit by pairing with a dominant partner [Ekman 1990; Lemmon et al. 1997]); (b) adults have higher pair fidelity rates (i.e., the probability of remaining faithful to last year's partner) than do yearlings (e.g., Ens et al. 1993; Choudhury 1995; Pampus et al. 2005; Llambias et al. 2008); and (c) individuals that were faithful to their previous partner have higher pair fidelity rates than those that changed partner because birds that have found the best possible partner, either in terms of quality ("better option" hypotheses, Ens et al. 1993), or compatibility ("compatibility hypothesis," Choudhury 1995) should tend to stay with them. We then use simulated capture histories with known parameter values to test the model performance under different values of state-dependent recapture rates. Finally, we demonstrate that this modeling framework is readily applicable to other dyadic interactions, and consider several possible extensions and applications of the framework, as well as discussing its limitations.

Methods

Multievent model framework for estimating pair fidelity

In MECMR models, individuals move independently among a finite set of mutually exclusive states, over a finite set of capture occasions (Pradel 2005). At each capture occasion, an event is observed. Events are related to the true, but not necessarily known, state of the individual through a series of conditional probabilities (Pradel et al. 2008; Choquet et al. 2009b). The general MECMR model for estimating pair fidelity we developed here uses three exclusive states: (1) Alive with the same partner (state "AS"): the focal individual is alive and breeding with its partner from the previous year; (2) Alive with a different partner (state "AD"): the focal individual is alive and breeding with a different partner to the previous year; and (3) Dead (state "D"): the focal individual is dead (this state is unobservable, but explicitly included in all multievent models). An individual can occupy only one state in a given breeding season. Transitions among these three states (i.e., "AS", "AD", "D") are modeled as a two-step process composed of the probability of survival over the annual time interval, followed by the probability of transitioning among live states (i.e., transitions among states are conditional on survival over the time period, see Fig. 1).

The capture histories of individuals are coded as a series of observed events (Fig. 1). Events contain information on the capture of the focal individual combined with information on its pair status, which is in turn determined using additional information on the capture histories of current and previous partners of the focal individual, as well as knowledge of their pair status. Using this information, we defined seven exclusive events that could be observed at each capture occasion:

- event 0 = the focal individual is not captured in the current breeding season (i.e., at t), its partner from the previous season ($t - 1$) is either not captured at $t - 1$ or t, or is captured breeding at t at an active nest with an unknown partner;
- event 1 = the focal individual is captured at t, and is breeding with its partner from $t - 1$;
- event 2 = the focal individual is captured at t but is breeding with a different partner to that from $t - 1$;
- event 3 = the focal individual is captured at t but it is not known whether its current partner, which is captured, is the same as the one from $t - 1$;
- event 4 = the focal individual is captured at t, its current partner is not captured, but its partner from $t - 1$ is captured at t at a different nest (and hence is not breeding with the focal individual at t);
- event 5 = the focal individual is captured at t, its current partner is not captured, and its partner from $t - 1$ is either not captured in t or was not known in $t - 1$;
- event 6 = the focal individual is not captured at t (and hence its current partner is unknown), but its

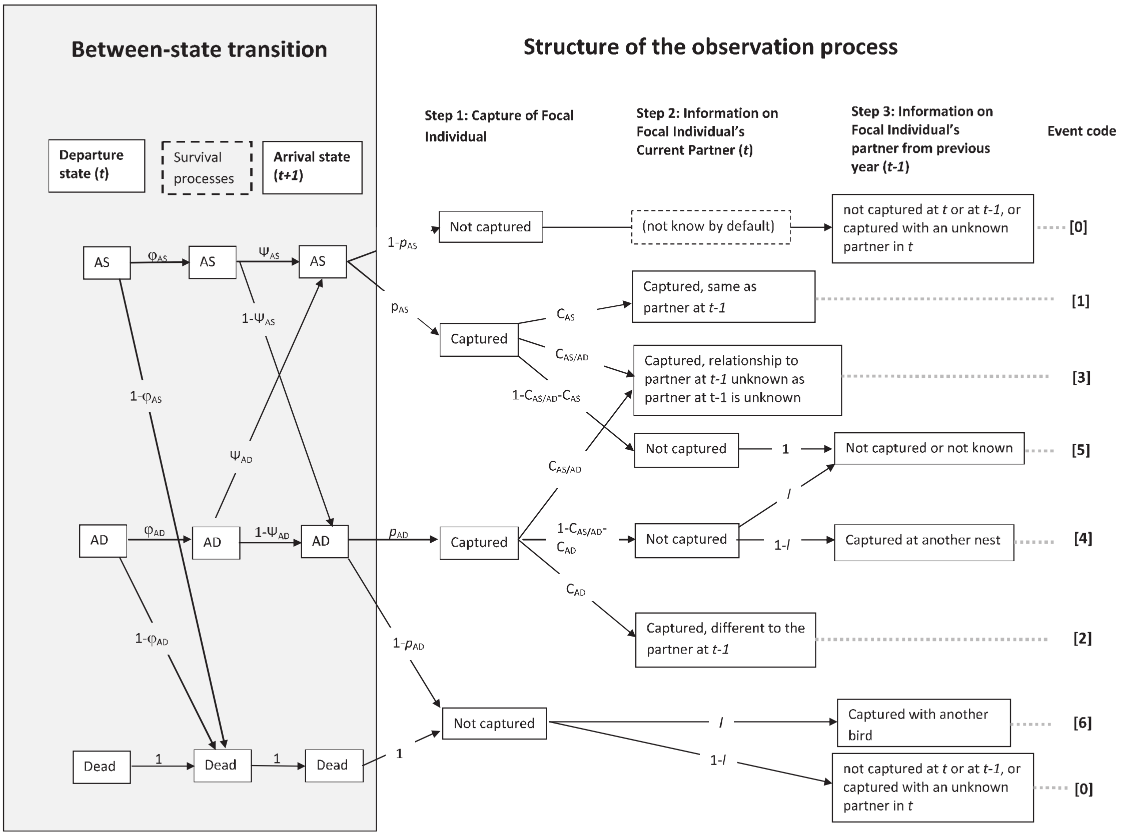

Figure 1. Illustrative figure of the between-state transition process and the structure of the observation process used to estimate pair fidelity rates. Three possible states are "AS," alive and breeding with the previous year partner; "AD," alive and breeding with a partner different to the previous year one; "D," dead (cannot appear for the initial capture of individuals). Between-state transition process has two steps: survival (ϕ_{AS}, survival probability for individuals in the state "AS"; ϕ_{AD}, survival probability for individuals in the state "AD") and transition among live states, conditional on survival ($\psi_{AS\text{->}AS}$, probability of staying with the same partner for individuals in the state "AS"; $\psi_{AD\text{->}AS}$, probability of staying with the same partner for individuals in the state "AD"). Observation process is composed of three steps: capture of the focal individual, information on focal individual's current partner, and information on focal individual's previous year partner. Event codes used to construct the capture histories of focal individuals are given in squared brackets. Probability parameters are given above the arrows and explained in more detail in the "Methods" section.

partner from $t - 1$ is captured breeding with another individual at t.

These seven events are the most general case of event construction for this type of dyadic association. Events 1, 2, and 4 are possible only under a single underlying state, while the remaining events are possible under multiple states (see Fig. 1 for further details).

Specification of parameters and the model structure

Following notation in Pradel (2005) our model is defined with three types of parameters: (1) initial state probabilities π, represented in a vector of probabilities, Π; (2) transition probabilities involving: survival probabilities, ϕ (represented in the survival matrix, Φ), and between-state transition probabilities, ψ (conditional on survival, and represented in the transition matrix, ψ); and (3) event probabilities. Event probabilities are conditional on the underlying state, that is, p(event | state), and are composed of (a) the recapture probability of the focal individual p (i.e., p(focal capture status | state), represented in the matrix, P); (b) the capture probability of its current partner c, conditional on the capture of the focal individual (i.e., p(focal partner status | focal capture status), represented in the matrix, P2); and (c) the capture probability of the previous year's partner l, incorporating knowledge of its pairing status in the current year (p(event | focal partner status), represented in the matrix, P3). These three event matrices connect an observed event with the underlying state, such that:

$$p(\text{event} \mid \text{state}) = p(\text{focal capture status} \mid \text{state}) \times p(\text{focal partner status} \mid \text{focal capture status}) \times p(\text{event} \mid \text{focal partner status}) \tag{1}$$

or, alternatively

$$p(\text{event} \mid \text{state}) = \mathrm{P} \times \mathrm{P2} \times \mathrm{P3} \tag{2}$$

The vector of initial state probabilities (eq. 3) is composed of two elements representing two possible states (“AS” or “AD”) at the time of first capture of the individual. The state dead is not possible at the first capture, and thus has probability zero.

$$\Pi = \begin{array}{ccc} \mathrm{AS} & \mathrm{AD} & \mathrm{D} \\ \hline \pi_{\mathrm{AS}} & 1-\pi_{\mathrm{AS}} & 0 \end{array} \tag{3}$$

The rows of the survival matrix (eq. 4) specify the state (“AS” or “AD”) an individual is at the time t, as indicated in the first column. The elements of this matrix represent the probabilities that an individual in a given state at time t will survive (ϕ_{AS} is survival probability of an individual in the “AS” state and ϕ_{AD} of individual in the “AD” state) or die ($1-\phi_{\mathrm{AS}}$, $1-\phi_{\mathrm{AD}}$) between t and $t+1$, with the arrival state (“AS,” “AD,” “D”) indicated in the row above the matrix.

$$\Phi = \begin{array}{cccc} & \mathrm{AS} & \mathrm{AD} & \mathrm{D} \\ \hline \mathrm{AS} & \phi_{\mathrm{AS}} & 0 & 1-\phi_{\mathrm{AS}} \\ \mathrm{AD} & \phi_{\mathrm{AD}} & 1-\phi_{\mathrm{AD}} & \\ \mathrm{D} & 0 & 0 & 1 \end{array} \tag{4}$$

The rows of the transition matrix (eq. 5) specify the state an individual is at time t (as indicated in the first column), while the columns specify its state at time $t+1$ (as indicated in the row above the matrix). The elements of this matrix are transition probabilities from states at time t to states at time $t+1$, conditional on the survival over the time period.

$$\psi = \begin{array}{cccc} & \mathrm{AS} & \mathrm{AD} & \mathrm{D} \\ \mathrm{AS} & \psi_{\mathrm{AS}\to\mathrm{AS}} & 1-\psi_{\mathrm{AS}\to\mathrm{AS}} & 0 \\ \mathrm{AD} & \psi_{\mathrm{AD}\to\mathrm{AS}} & 1-\psi_{\mathrm{AD}\to\mathrm{AS}} & 0 \\ \mathrm{D} & 0 & 0 & 1 \end{array} \tag{5}$$

Rows of the matrix P (eq. 6) correspond to the columns of the between-state transition matrix, and represent the state an individual is in at t. Columns of this matrix define whether the focal individual is captured (FC) or not (FNc) given its underlying state (indicated with a superscript after FC and FNc). Thus, p_{AS} and p_{AD} are capture probabilities for individuals in the state “AS” or “AD,” respectively.

$$\mathrm{P} = \begin{array}{cccccc} & \mathrm{FNc}^{\mathrm{AS}} & \mathrm{FNc}^{\mathrm{AD}} & \mathrm{FNc}^{\mathrm{D}} & \mathrm{FC}^{\mathrm{AS}} & \mathrm{FC}^{\mathrm{AD}} \\ \hline \mathrm{AS} & 1-p_{\mathrm{AS}} & 0 & 0 & p_{\mathrm{AS}} & 0 \\ \mathrm{AD} & 0 & 1-p_{\mathrm{AD}} & 0 & 0 & p_{\mathrm{AD}} \\ \mathrm{D} & 0 & 0 & 1 & 0 & 0 \end{array} \tag{6}$$

The matrix P2 (eq. 7) describes the combined probability of capturing the focal individual’s current partner and knowing its identity in relation to the focal individual’s previous partner (i.e., same as, or different to previous partner), conditional on the capture of the focal individual. The rows of matrix P2 correspond to the columns of matrix P. Elements of the matrix P2 define probabilities that the current partner is captured (PC) or not captured (PNc), or whether the current partner is captured but it is not known if it is the same or different to the one in the last year (PNn). Superscripts specify the underlying state of the focal individual. $1-\sum C$ represents the complement to the sum of other parameters in the same row. Columns PNc$^{\mathrm{AS}}$ and PNc$^{\mathrm{AD}}$ appear in the matrix twice, because the two on the left side of the matrix correspond to capture of the current partner when the focal is not captured (and this equals 1), while the two on the right side correspond to the capture of the current partner when the focal is captured. It was necessary to structure P2 matrix in this way to allow the construction of the P3 matrix.

$$\mathrm{P2} = \begin{array}{ccccccccc} & \mathrm{PNc}^{\mathrm{AS}} & \mathrm{PNc}^{\mathrm{AD}} & \mathrm{PNc}^{\mathrm{D}} & \mathrm{PC}^{\mathrm{AS}} & \mathrm{PC}^{\mathrm{AD}} & \mathrm{PNn}^{\mathrm{AS,AD}} & \mathrm{PNc}^{\mathrm{AS}} & \mathrm{PNc}^{\mathrm{AD}} \\ \hline \mathrm{FNc}^{\mathrm{AS}} & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathrm{FNc}^{\mathrm{AD}} & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathrm{FNc}^{\mathrm{D}} & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ \mathrm{FC}^{\mathrm{AS}} & 0 & 0 & 0 & C_{\mathrm{AS}} & 0 & C_{\mathrm{AS/AD}} & 1-\Sigma C & 0 \\ \mathrm{FC}^{\mathrm{AD}} & 0 & 0 & 0 & 0 & C_{\mathrm{AD}} & C_{\mathrm{AS/AD}} & 0 & 1-\Sigma C \end{array} \tag{7}$$

Finally, matrix P3 (eq. 8) describes the probability of capturing the focal individual’s partner from the previous breeding season ($t-1$) in the current capture occasion

(t), incorporating information on its pairing status at time t. Note that if the focal individual's current partner was breeding with another individual than the focal at $t-1$, then this indicates partner change. The rows of matrix P3 correspond to the columns of matrix P2. The column numbers correspond to the event codes (see above and Fig. 1).

$$\mathrm{P3} = \begin{array}{r|ccccccc} & 0 & 1 & 2 & 3 & 4 & 5 & 6 \\ \hline \mathrm{FNc}^{\mathrm{AS}}, \mathrm{PNc}^{\mathrm{AS}} & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ \mathrm{FNc}^{\mathrm{AD}}, \mathrm{PNc}^{\mathrm{AD}} & 1-l & 0 & 0 & 0 & 0 & 0 & l \\ \mathrm{FNc}^{\mathrm{D}}, \mathrm{PNc}^{\mathrm{D}} & 1-l & 0 & 0 & 0 & 0 & 0 & l \\ \mathrm{FC}^{\mathrm{AS}}, \mathrm{PC}^{\mathrm{AS}} & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ \mathrm{FC}^{\mathrm{AD}}, \mathrm{PC}^{\mathrm{AD}} & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ \mathrm{FC}^{\mathrm{AD,AS}}, \mathrm{PNn}^{\mathrm{AS,AD}} & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ \mathrm{FC}^{\mathrm{AS}}, \mathrm{PNc}^{\mathrm{AS}} & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ \mathrm{FC}^{\mathrm{AD}}, \mathrm{PNc}^{\mathrm{AD}} & 0 & 0 & 0 & 0 & 1-l & l & 0 \end{array} \tag{8}$$

Application of the MECMR to great tit breeding data

To demonstrate the utility of this MECMR modeling framework for estimating pair fidelity rates, we applied the model to 30 years of breeding records (1980–2009) from a long-term monitored population of great tits breeding in nest boxes. Around 1020 nest boxes are distributed at variable densities within the c. 385 ha mixed deciduous woodland of Wytham Woods, Oxfordshire, U.K. During the synchronous breeding season (April–May), nest boxes were visited on a weekly basis to collect data on breeding attempts. Individuals were captured between days 6 and 14 of the nestling phase either within the nest box by hand or using traps, or with mist-nets in front of the box. All captured individuals and all nestlings that survived to day 15 were marked with unique metal rings. The sex of parents was determined based on the presence (female) or absence (male) of a brood patch. Age (either yearling or adult, 2+ years old) was determined from plumage characteristics (Svensson 1992) or ringing records.

Capture histories for individuals (coded according to the seven events described above) were obtained for 4784 females and 4430 males, comprising 7837 breeding attempts. Both parents were captured in 84.5% of breeding attempts. In 12.9% of breeding attempts only the female was captured, and in the remaining 2.6% only the male was captured. To avoid issues of statistical nonindependence in analyses, the MECMR framework was applied to capture histories of males and females separately. MECMR models were built in E-SURGE Version 1.8.5 (Choquet et al. 2009b; Choquet and Nogue 2011). Implementation details are given in the Data S1 (Section 1). We assessed the identifiability of this model in E-SURGE with simulated datasets and with our data according to methods described in Choquet and Cole (2012). To ensure convergence of models on the global minima, models were run using repeated random initial values.

Model covariates and model selection process

Currently, there is no specific goodness-of-fit (GOF) test for MECMR models. Thus, we assessed the fit of the general mark–recapture assumptions to our data by assessing the GOF of the single state Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965), which allows for full time variation and no age effect in survival and recapture rates (Choquet et al. 2009a). The CJS model assumes all animals present at the same sampling occasion have equal future survival and recapture probabilities regardless of past history and capture in the current sampling occasion. These assumptions were tested using program U-CARE (Choquet et al. 2005, 2009a).

Starting models in both analyses (for males and females) allowed for time and state dependence in recapture probability of the focal individual, and for state, time, and age (yearlings and adults) dependence in survival and transition probabilities. Variation by state was restricted to adults only, as yearling birds have never previously bred and their survival and transition rates cannot depend on their current pair status. The initial state for all individuals was arbitrarily chosen to be "AD," and fixed accordingly.

We used a 3-stage model selection process (Grosbois and Tavecchia 2003). First, we modeled recapture rates as constant, or as varying in relation to state, or time (yearly variation), while keeping survival and transition rates fully parameterized. Next, we used the best recapture rate model identified in the first stage (i.e., the model with the lowest Akaike Information Criteria [AIC]), to model survival rates as constant, or as varying in relation to state, age, and time. Finally, with recapture and survival rates parameterized according to the best models identified above, we modeled transition rates as constant, or varying in relation to age, time, and departure state (the state an individual transitions from). We considered additive effects of all these variables (time, age, state) on rate parameters and included interactions where we considered that these were biologically sensible (see Table S1). In total we performed model selection on a candidate list of four different recapture, ten different survival, and eleven different transition rate models (see Table S1 for full listing). Model selection was based on AIC (Anderson and Burnham 2002). Normalized AIC weights (w_i) were used as a measure of relative support for each model.

Evaluating model performance on the simulated capture histories

We evaluated the ability of our new modeling framework to estimate state-dependent survival and fidelity rates, under varying recapture rates using simulated capture histories. We also compared the accuracy of the pair fidelity rates obtained by our new model to those obtained by the traditional method (which ignores imperfect detectability and capture heterogeneity and where only definitive cases of fidelity and partner change can be considered). We simulated three separate capture history datasets consisting of 6400 capture histories, over 10 sampling occasions, under state-dependent but varying recapture rates (recapture probabilities of birds in the state "AD" for three simulations were 0.5, 0.7, and 0.8, while the recapture rate for birds in state "AS" was 0.9). The values of all other parameters were chosen to reflect the values obtained from our great tit dataset (ignoring temporal variation), and were kept the same in all three simulations ($\phi_{AS} = 0.6$, $\phi_{AD} = 0.4$; $\psi_{AS} = 0.4$; $\psi_{AD} = 0.3$; c_{AS} and $c_{AD} = 0.73$; $c_{AS/AD} = 0.13$, $l = 0.92$).

To estimate parameters using the MECMR modeling framework, we ran a model in which survival and transition rates were dependent on the state of departure, with recapture rates dependent on the state of arrival. To calculate pair fidelity rates using the traditional method, we applied the following equation:

$$\psi_{\mathrm{TRAD}} = \mathrm{f}/(\mathrm{f} + \mathrm{ch}) \qquad (9)$$

where f is the number of times event 1 occurred (definite case of pair fidelity) and ch is the number of times events 2 and 4 occurred (definite cases of partner change). To calculate pair fidelity rates of birds breeding with the same partner as in $t - 1$ we applied equation 9 to birds that were recorded in event 1 at t and in events 1, 2, or 4 at $t + 1$. To calculate pair fidelity rates of birds breeding with a different partner to that at $t - 1$, we applied equation 9 to birds that were recorded in events 2 or 4 at t and in events 1, 2, or 4 at $t + 1$.

Results

The results of the GOF tests revealed no detectable lack of fit of the CJS model in either dataset (females: $\chi^2 = 80.10$, df = 91, $P = 0.786$; males: $\chi^2 = 76.14$, df = 99, $P = 0.957$), indicating that the general assumptions of the CJS model were reasonably met for both datasets. In addition there was no evidence for overdispersion in either dataset (females: $\hat{c} = 0.88$; males: $\hat{c} = 0.88$).

For both sexes, there was strong support for models in which recapture rates were constant over the study period but varied by state (i.e., pair status, Tables 1 and 2). Individuals that were faithful to the previous year's partner were more likely to be recaptured than were individuals that had changed partners (recapture rate: faithful females = 0.72, CI = 0.69–0.76, changed partner females = 0.65, CI = 0.63–0.67, faithful males = 0.61, CI = 0.57–0.64, changed partner males = 0.55, CI = 0.53–0.57, Fig. S1). For both sexes, the best supported model in the

Table 1. Summary results of the multievent mark–recapture analysis to estimate recapture, survival, and pair fidelity rates in female great tits.

	Model Structure							
Parameter	p	ϕ	ψ		dev	AIC	Δ_i	w_i
Recapture rates (p)	state	state*Ad+Age**t*	state*Ad+Age**t*	128	31561.86	31817.86	0	0.99
	c			127	31575.12	31829.12	11.26	0.00
	state+*t*			156	31530.10	31842.10	24.24	0.00
	t			155	31544.65	31854.65	36.79	0.00
Survival rates (ϕ)	state	state*Ad+Juv+*t*	Age**t*+state*Ad	100	31597.62	31800.00	0	0.99
		state*Ad+Age**t*		128	31561.86	31820.23	20.23	0.00
		Age+*t*		99	31678.40	31878.78	78.78	0.00
		state*Ad+Juv		72	31792.08	31938.45	138.45	0.00
		state+*t*		99	31752.46	31952.83	152.83	0.00
Transition rates (ψ)	state	state*Ad+Juv+*t*	state*Ad+Juv+*t*	72	31624.86	31768.85	0	0.80
			Age+*t*	71	31629.78	31771.78	2.92	0.18
			state+*t*	71	31634.80	31776.80	7.95	0.00
			t	70	31651.85	31791.85	22.99	0.00
			state*Ad+Age**t*	100	31597.62	31797.62	28.77	0.00

For survival and transition rate models, only the top five models are shown. See Table S1 for model notation. np, number of estimable parameters, dev, deviance; AIC, Akaike information criterion; Δ_i, the AIC difference between the current model and the model with the lowest AIC value; w_i, Akaike weight; state, state dependent rates; c, constant rates; *t*, time-dependant rates; Age, age-dependent rates; Ad, dependence of rates for adult birds (2+ years old) only; Juv, dependence of rates for first year breeders only; +, additive effect of variables; *, interactive effect of variables

Table 2. Summary results of the multievent mark–recapture analysis to estimate recapture, survival, and pair fidelity rates in male great tits.

	Model Structure							
Parameter	p	ϕ	ψ		dev	AIC	Δ_i	w_i
Recapture rates (p)	state	state*Ad+Age**t*	state*Ad+Age**t*	128	26838.48	27094.48	0	0.89
	c			127	26844.74	27098.74	4.26	0.11
	state+*t*			156	26798.26	27110.26	15.78	0.00
	t			155	26804.68	27114.68	20.20	0.00
Survival rates (ϕ)	state	state*Ad+Juv+*t*	Age**t*+state*Ad	100	26876.58	27076.58	0	0.99
		state*Ad+Age**t*		128	26838.48	27094.48	17.9	0.00
		Age+*t*		99	26958.19	27156.19	79.62	0.00
		Age**t*		127	26915.19	27169.19	92.62	0.00
		state*Ad+Juv		72	27050.88	27194.88	118.31	0.00
Transition rates (ψ)	state	state*Ad+Juv+*t*	state*Ad+Juv+*t*	72	26904.92	27048.92	0	0.99
			Age+*t*	71	26917.67	27059.67	10.75	0.00
			state+*t*	71	26922.61	27064.61	15.69	0.00
			state*Ad+Juv	44	26984.61	27072.61	23.69	0.00
			state*Ad+Age**t*	100	26876.58	27076.58	27.66	0.00

For survival and transition rate models, only the top five models are shown. See Table S1 for model notation. np, number of estimable parameters, dev, deviance; AIC, Akaike information criterion; Δ_i, the AIC difference between the current model and the model with the lowest AIC value; w_i, Akaike weight; state, state dependent rates; *c*, constant rates; *t*, time-dependant rates; Age, age-dependent rates; Ad, dependence of rates for adult birds (2+ years old) only; Juv, dependence of rates for first year breeders only; +, additive effect of variables; *, interactive effect of variables

candidate set allowed survival rates to vary with time, age, and by state (i.e., according to pair status of adults, Tables 1 and 2). As predicted, birds that remained with their previous partner had higher annual survival rates than birds that had changed partners (Fig. 2A and B). For both sexes, the best supported transition rate model allowed annual pair fidelity rates to differ between adults and yearlings, and to vary over time (Tables 1 and 2). Importantly, this best supported model also allowed transition rates to differ according to the pair status of adult birds (Tables 1 and 2). Adults that had bred with their current partner in the previous year displayed greater pair fidelity rates than did adults that had not bred with their current partner in the previous year (i.e., the probability of transitioning from state "AS" to state "AS" was higher than the probability of transitioning from state "AD" to "AS," Fig. 2C and D).

Application of the the MECMR to the three simulated datasets (with different recapture rates of birds in the "AD" state), revealed that our model correctly estimated (with very little bias) all of the input parameters (Table 3). More importantly, the MECMR model estimated pair fidelity rates far more accurately than did the traditional method in each of the three datasets, and this was particularly evident in the first simulated dataset where recapture was lowest (Table 3).

Discussion

Traditional means of estimating rates of pair fidelity in wild populations, where recapture rates are generally low and potentially heterogeneous can, in principle, lead to flawed biological inferences based on these rates. The novel multievent mark–recapture modeling framework we developed here overcomes these problems and thus allows robust and unbiased estimates of pair fidelity rates. The model has an additional advantage in allowing statistical exploration of heterogeneity in state transitions, and the covariation between these; something that is impossible using raw observations alone. We demonstrated the application of this framework to a 30-year great tit breeding data and showed that faithful birds display higher recapture rates and experience higher survival and fidelity rates compared with birds that change partners. The strong support for state-dependent parameters reveals that traditional estimates that ignore this variation are likely to be biased and also suggest that there might be large fitness costs associated with partner change in this system.

Our results provide the first evidence, to our knowledge, that pair status (i.e., breeding with the same partner or different partner in $t-1$ and t) can influence recapture rates. While the importance of accounting for capture heterogeneity according to traits such as sex (Tavecchia et al. 2001; Lachish et al. 2011), age (Tavecchia et al. 2001; Bouwhuis et al. 2012), breeding status (Cam et al. 2002; Grosbois and Thompson 2005), dominance (Cubaynes et al. 2010), and infection status (Lachish et al. 2011) has already been emphasized, pair status as a source of capture heterogeneity has not previously been considered. The only related work of which we are aware is that of Klaich et al. (2011), who developed a likelihood-based model where capture rates of individuals

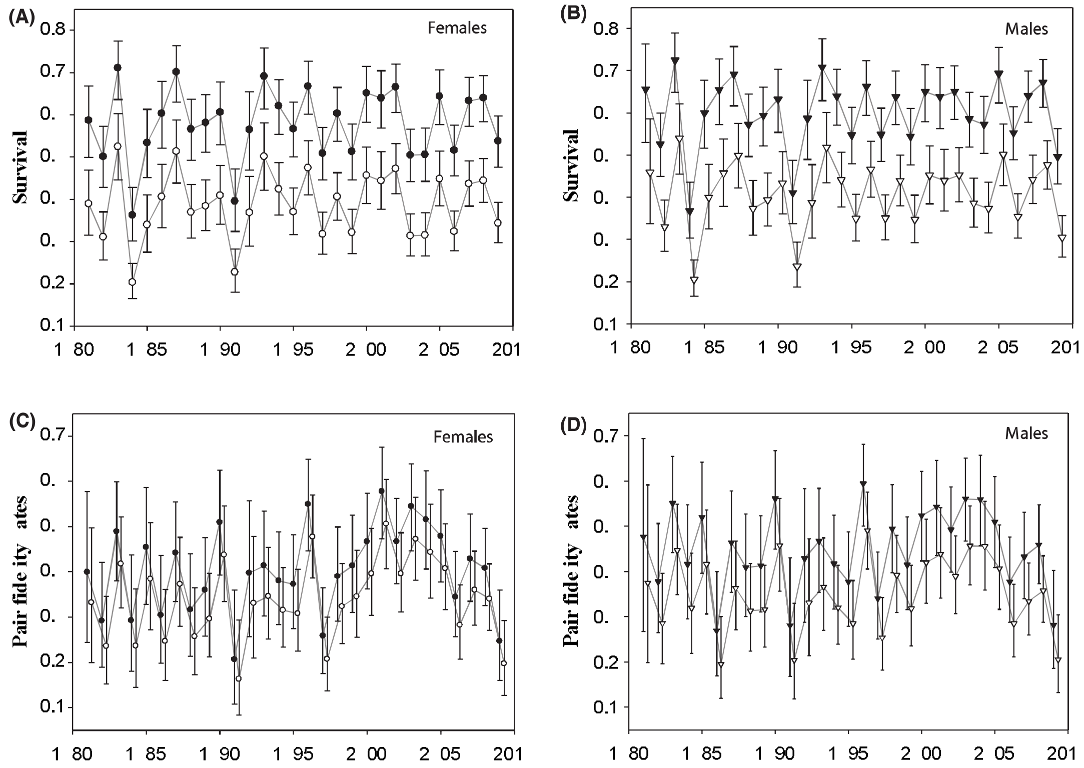

Figure 2. Survival rates (±95% CI) for (A) adult female and (B) adult male great tits by pair status (estimates obtained from best supported model for each sex, see Tables 1 and 2) and pair fidelity rates (±95% CI) for adult (C) female and (D) male great tits (estimates obtained from best supported model for both sexes, see Tables 1 and 2). Filled symbols show rates for individuals that remained with their previous partner (state "AS") while open symbols show rates for individuals that changed partners (state "AD").

Table 3. Results of simulation analyses to assess the efficacy of the MECMR model to estimate state-dependent rates and the accuracy of both the new MECMR model and the traditional method to estimate pair fidelity rates.

Method		MECMR			Traditional method
Simulations	State	p	ϕ	ψ	ψ
Dataset 1	"AS"	0.884	0.572	0.422	0.616
	"AD"	0.470	0.411	0.283	0.410
Dataset 2	"AS"	0.902	0.586	0.405	0.507
	"AD"	0.687	0.406	0.288	0.346
Dataset 3	"AS"	0.888	0.609	0.388	0.405
	"AD"	0.781	0.397	0.303	0.339

Estimates of the recapture rates (p), survival rates (ϕ), and fidelity rates (ψ) were obtained for birds breeding with the same partner as in the previous year (state "AS") and those breeding with a different partner to the last year (state "AD"). Datasets were simulated using the following values ($\phi_{AS} = 0.6$, $\phi_{AD} = 0.4$; $\psi_{AS} = 0.4$; $\psi_{AD} = 0.3$; $p_{AS} = 0.9$, c_{AS} and $c_{AD} = 0.73$; $c_{AS/AD} = 0.13$, $l = 0.92$; see text for details) and with p_{AD} set to 0.5 (Dataset 1), 0.7 (Dataset 2), or 0.8 (Dataset 3).

in dyads (of a demographically closed population) varied between individuals that are associated and those that are not associated at the capture occasion *t*. The lower recapture rates for birds that changed partners between breeding seasons in this study might be a consequence of early breeding failure (e.g., Hannon and Martin 1996; Flynn et al. 1999), because birds were captured at a relatively late stage of the breeding cycle (when chicks were 6–14 days old). Alternatively, this pattern might result from differences in the chick provisioning rates or other behaviors of faithful pairs and pairs that had not bred together (Green 2002; Moody et al. 2005). Regardless of the underlying mechanisms, the existence of capture heterogeneity will bias estimates of pair fidelity obtained by methods that do not account for it, and argues against the use of traditional methods of estimating pair fidelity in wild populations.

A key advantage of the MECMR modeling framework developed in this study is that both fidelity and survival rates can be obtained in a single analysis and variation in these vital rates can be modeled as a function of pair status. These features allowed us to test hypotheses regarding the dynamics and fitness benefits of pair fidelity in the studied population. As predicted, our analyses revealed that faithful individuals experienced substantially higher survival rates than did individuals that changed partners between consecutive breeding seasons. Although it has been suggested that birds retain their partners so as to avoid potential survival costs (Ekman 1990; Pampus et al. 2005), we are aware of only one study that has provided empirical support for (or even tested for) this possibility (Nicolai et al. 2012). Our finding lends further support for possible survival cost associated with partner change.

Our results also agree with the common finding that pair fidelity rates are higher for adults than for yearlings (e.g., Pampus et al. 2005; Llambias et al. 2008). This pattern is usually attributed to yearling birds making more errors in initial mate choice (Choudhury 1995), placing higher importance on finding a better partner as they have more years to breed ahead (Choudhury 1995), and/or being left by their partners or expelled by another bird more often (Ens et al. 1993; Choudhury 1995) compared to adult birds. Traditional methods of analyzing pair fidelity rates utilize post hoc tests to assess such differences. The MECMR framework and model selection approach presented here is a more rigorous and powerful statistical method for such analyses. This approach also allowed us to demonstrate that birds breeding with the same partner at $t-1$ and at t, were more likely to remain in the faithful state at $t+1$, supporting the hypotheses that individuals that have found an acceptable partner (whether in terms of quality or compatibility, where compatibility can be genetic, Zeh and Zeh 1997; Hansson and Westerberg 2002; morphological, Black et al. 2007; behavioral, Spoon et al. 2006; or hormonal) tend to remain with them (Choudhury 1995). The finding that fidelity rates vary according to pair status (i.e., are state dependent) suggests that traditional estimates of pair fidelity rates may be biased and that inferences regarding the costs and benefits of pair fidelity based on them may be unreliable. The results of our simulation analyses strongly supported this suggestion, showing that traditional estimates of pair fidelity obtained in the presence of capture heterogeneity were inaccurate and biased.

Utility and further applications of this MECMR modeling framework

The findings discussed above, while likely to be system specific, clearly highlight the potential of this new MECMR modeling framework to explore the causes, costs, and benefits of pair fidelity. The modeling framework easily accommodates the inclusion of external covariates (e.g., population density, sex ratio, or abiotic factors) and individual covariates (e.g., morphological or behavioral traits), which extend the range of hypotheses regarding the causes and consequences of pair fidelity that can be tested. Moreover, the MECMR model can be extended to include new states (e.g., "same partner/high quality territory", "same partner/low quality territory" or "same partner/same territory", "same partner/different territory", etc.) to evaluate the relationship between fidelity and territory quality, or assess whether fidelity to a partner is driven by fidelity to a territory. Extension of the modeling framework would also allow state transitions to be modeled as higher order Markovian process (so-called memory models, as per Hestbeck et al. 1991), allowing the influence of past breeding experience on future pairing decisions to be analyzed (Rouan et al. 2009).

Our MECMR model was developed to assess rates of fidelity in pair-bonded individuals but can be applied to other dyadic associations where members of associating pairs are (i) not members of a breeding pair, for example to assess parent–offspring provisioning rates; (ii) individual and a particular location, for example to assess fidelity to a feeding patch or roosting site; (iii) an individual and a group this individual associates with, for example, to assess rates at which individuals change group membership; (iv) two groups of individuals, for example, to assess attachment of a certain type of pollinator to a certain type of plant. It is important to note, however, that care must be taken to avoid pseudo-replication. If the associating individuals belong to two discrete and distinguishable classes that remain unchanged over the study period (i.e., male and female, different species), then pseudo-replication can be avoided by analyzing association rates in the two classes separately (as was done in our analysis of pair fidelity in great tits). In other situations, reducing the length of the study period to ensure individuals remain in a single class (e.g., parent feeding a chick during one breeding season) can alleviate problems of pseudo-replication.

Limitations of the MECMR approach

In all mark–recapture analyses, including MECMR models, mortality is confounded with permanent emigration. Our finding of lower survival rates for great tits that changed partners might thus be a consequence of higher rates of breeding dispersal for these individuals. A few previous studies on great tits have shown that breeding dispersal is generally lower for faithful birds compared to those that have changed partner (Andreu and Barba 2006; and references therein). Hence, we cannot discount the possibility that differential emigration drives the difference in apparent survival rates between faithful individuals and those that changed partners in our case study population. Where additional information on recoveries or resightings of marked individuals from a larger peripheral area is available, the joint analysis of such data in a MECMR framework can, under certain assumptions, allow for separating survival from emigration (Juillet et al. 2011). Another limitation of the MECMR model we present here is that estimates of pair fidelity are confounded with mortality of the focal individual's partner, which constrains interpretation of the results in terms of individual choice. An individual whose partner dies between breeding seasons must breed with a new partner even if the previous partner was the preferred one. We found that faithful great tits of both sexes (and hence, both members of faithful pairs) experienced higher survival rates than did individuals that changed partners. Consequently, members of faithful great tit pairs will have a greater opportunity to remain together from one breeding season to the next. Further development and extension of the MECMR framework to include additional states separating widowed and divorced individuals, could provide a means of investigating how two different strategies (stay with a partner or divorce) are adopted by individuals in the population in relation to different ecological and social factors. Nevertheless, if we assume that widowing rates are related to mortality rates, then we can estimate divorce rates from the vital rate estimates produced by the MECMR model (although only for individuals in the "AS" state). For example, in our great tit population, the divorce rate for females in state "AS" ($d_{\text{AS\_female}}$) can be calculated from their fidelity rate ($\psi_{\text{AS\_female}}$) and the mortality rate of males in state "AS" ($1-\phi_{\text{AS\_male}}$):

$$\begin{aligned} d_{\text{AS\_female}} &= 1 - \psi_{\text{AS\_female}} - (1 - \phi_{\text{AS\_male}}) \\ &= \phi_{\text{AS\_male}} - \psi_{\text{AS\_female}}. \end{aligned}$$

This is possible because the partners of "AS" females are "AS" males, for which we have mortality estimates. On the other hand, for individuals in the state "AD" we can only obtain approximate divorce rates, as we cannot tell at which rates their partners die (their partners can either be other adult birds in the state "AD," or yearling birds, and these two classes have different mortality rates).

In conclusion, we have shown that, compared to previously used methods, the MECMR framework we have developed is not only able to provide parameter estimates accounting for capture heterogeneity and without discarding partial information, but also allows, either in its current form or using further extensions, an exploration of different evolutionary hypotheses on correlates, costs, and benefits of pair fidelity.

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Conflict of Interest

None declared.

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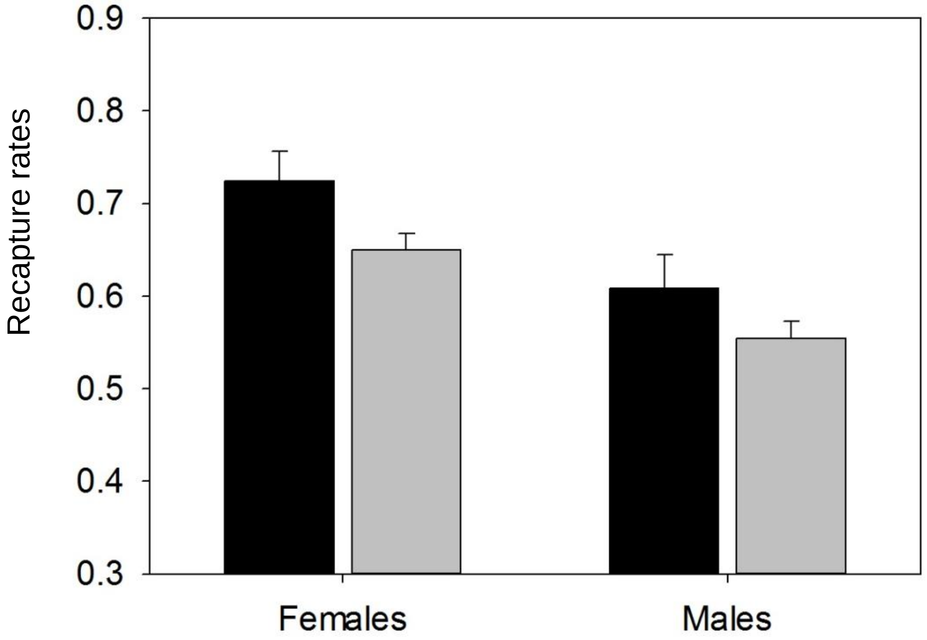
Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Using the program E-SURGE for fitting model of pair fidelity.

SUPPLEMENTARY FIGURE

Figure S1. Recapture rates for pair faithful (state ’AS’, black bars) and partner changed (state ‘AD’, grey bars) females and males with upper 95% CI.



SUPPLEMENTARY TABLE

Table S1. Model notation describing the recapture, survival and transition rate models included in the candidate list for multi-event mark–recapture modelling of survival and pair fidelity rates in great tits.

Recapture	Survival	Between-state transition
c	c	c
t	t	t
state	Age	Age
state+t	state	state
	Age+t	Age+t
	state+ t	state+t
	Age*t	Age*t
	state*Ad+Juv	state*Ad+Juv
	state*Ad+Juv+t	state*Ad+Juv+t
	state*Ad+Age*t	state*Ad+Age*t
		state*t

SUPPLEMENTARY INFORMATION to Chapters 3, 4, and 5: Using the program E-SURGE for fitting model of pair fidelity

Contents

1. Description of the general modelling framework

We have developed a multi-event mark-recapture model to assess annual rates of pair fidelity (i.e. breeding with the same partner as in the last year), partner change (i.e. breeding with the different partner to the last year partner), and survival, while explicitly accounting for imperfect detectability and heterogeneity in detection probabilities among individuals in different states (pair status). The model combines mark–recapture data with data from auxiliary breeding records to inform an individual’s state (pair status).

The states considered in the model are:

‘AS’ (Alive with the Same partner), the focal individual is alive and breeding with its partner from the previous year;

‘AD’ (Alive with a Different partner), the focal individual is alive and breeding with a different partner to its partner in the previous year;

‘D’ (Dead), the focal individual is dead;

The events we can observe are:

- event 0 = the focal individual is not captured in the current breeding season (i.e. at *t*), its partner from the previous season (*t*-1) is either not captured at *t-1* or *t* , or is captured breeding at *t* at an active nest with an unknown partner;
- event 1 = the focal individual is captured at *t*, and is breeding with its partner from *t-1*;
- event 2 = the focal individual is captured at *t* but is breeding with a different partner to that from *t-1*;
- event 3 = the focal individual is captured at *t* but it is not known whether its current partner is the same as the one from *t-1*;
- event 4 = the focal individual is captured at *t*, its current partner is not captured, and its partner from *t-1* is captured at *t* but at a different nest (and hence is not breeding with the focal individual at *t*);
- event 5 = the focal individual is captured at *t*, its current partner is not captured, and its partner from *t-1* is either not captured in *t* or was not known in *t-1*;
- event 6 = the focal individual is not captured at *t* (and hence its current partner is unknown), but its partner from *t-1* is captured breeding with another individual at *t*.

The parameters estimated by the model are:

φ, survival probability;

ψ, transition probability, conditional on survival;

p, recapture probability (of the focal individual);

c, capture probability of focal's current (*t*) partner, conditional on the capture of the focal individual. This parameter incorporates information on the capture of the current partner and its identity in relation to the focal individual's *t-1* partner. If *t*-1 partner is not known then, even if the current partner is captured, we cannot tell if it is the same as or different to *t*-1 partner.

However, if the focal's current partner was breeding with an individual other than the focal individual in *t*-1, then this indicates partner change;

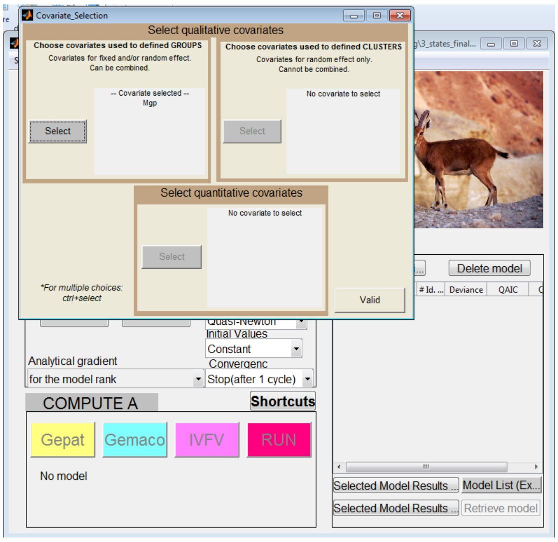
l, probability of capturing focal's *t*-1 partner at *t* (if *t*-1 partner is known) incorporating knowledge of its pairing status in *t*;

2. Fitting the pair fidelity model to the Wytham great tit capture histories (Chapter 3)

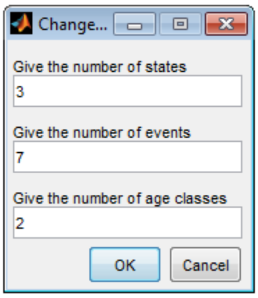
After starting E-SURGE the first step is to load the dataset consisting of capture histories and any covariates that have been included. The top of the dataset (in the Headed format) we used is shown below, where 'H:' stands for capture history, 'S:' stands for number of birds with a specific capture history (in our case each row is a capture history for one bird only); '$COV:Mgp' stands for the explanatory variable 'Marking group' :

```
 H:                               S:     $COV:Mgp
000003000000000000000000000000     1      Juv
000000036000000000000000000000     1      Ad
000000003600000000000000000000     1      Ad
000000360000000000000000000000     1      Juv
000003222000000000000000000000     1      Juv
000000300000000000000000000000     1      Juv
000000003000000000000000000000     1      Ad
```

As we have individuals that were captured as both yearlings and adults we include a covariate in the input file, which we labelled as 'Mgp' to indicate to which of the two Marking groups an individual belongs (individuals first captured breeding as yearlings are coded with 'Juv', individuals first captured as adults are coded as 'Ad'). Later we will use GEMACO code to obtain rates for the two age-classes we used in our study (yearlings and adults). When the data are loaded, a window asking you to choose covariates appears. Choose the first option (top left corner) by clicking the 'Select' button:



E-SURGE makes assumptions about the number of states and age classes. However, these need to be modified in our case. Change the number of states from 7 to 3 (i.e. ‘AS’, ‘AD’, ‘D’), and change the number of age classes to 2 by clicking the ‘Modify’ button on the main screen and then changing values in the corresponding boxes to look like this:



Give the number of states
3

Give the number of events
7

Give the number of age classes
2

In E-SURGE, models are built in several stages. First, the GEPAT (Generator of Pattern of elementary matrices) allows specifying the initial state vector and the transition and event matrices. GEPAT matrices are row stochastic, so the sum of all cell probabilities in each row must add to one. Thus, one cell probability in each row will be calculated as the complement of the others. This cell is denoted with ‘*’. There are some cells with a structural probability being equal to zero. These cells are denoted as ‘-‘. After specifying the matrices, the GEMACO (Generator of Matrix of Constraints) interface is used to constrain the parameters of interest to vary according to the model we are building, or the hypotheses we are testing.

2.1 Specifying the pattern matrices using the GEPAT interface

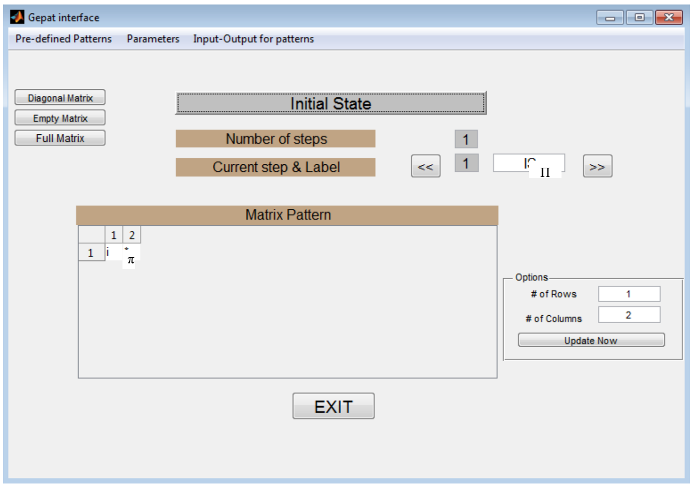
In this step we specify which parameters of the model will be estimated and which will be calculated as the complement of the other parameters. We also define those parameters that correspond to impossible events or transitions (fixed to zero).

To activate the GEPAT interface, click on the GEPAT button at the left bottom corner of the main window.

The initial state vector

The first matrix to appear in GEPAT is the matrix of the initial state probabilities which is composed of a single row with two states. The 'Dead' state cannot appear as the initial state.

$$\begin{array}{ccc} \text{AS} & \text{AD} & \text{D} \\ (\pi & 1-\pi & 0) \end{array}$$



Number of steps 1

Current step & Label 1 IS π

	1	2
1	i	* π

\# of Rows 1

\# of Columns 2

Later, at the IVFV stage, we have arbitrarily chosen to fix the probability of 'AD' to be 1 (i.e. the probability of 'AS' is then equal zero).

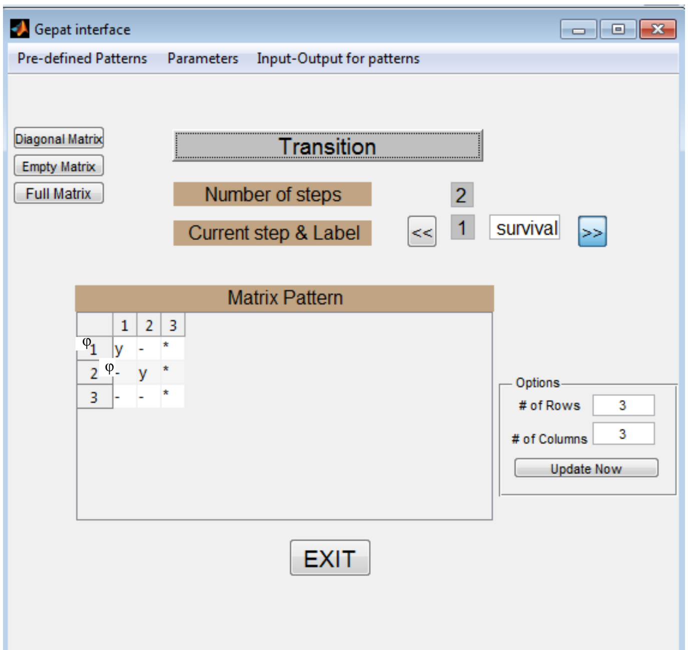
The matrices of survival and transition probabilities

We modelled the probability of transitioning between states as a two-step process composed first of the probability of survival over the yearly time interval and then the probability of transitioning among states (i.e. transitions among states are conditional on survival over the time-period). GEPAT initially offers only one step for transition. To increase the number of steps, enter ‘2’ in the box right to the ‘Number of steps’. We named the two transition matrices as ‘survival’ and ‘transition’.

The rows of the survival matrix specify the possible underlying states at time *t*.

Thus, we specify the survival matrix as follows:

$$\begin{array}{cc} & \begin{array}{ccc} \text{AS} & \text{AD} & \text{D} \end{array} \\ \begin{array}{c} \text{AS} \\ \text{AD} \\ \text{D} \end{array} & \begin{pmatrix} \varphi & 0 & 1-\varphi \\ 0 & \varphi & 1-\varphi \\ 0 & 0 & 1 \end{pmatrix} \end{array}$$



Number of steps: 2
Current step & Label: 1 survival

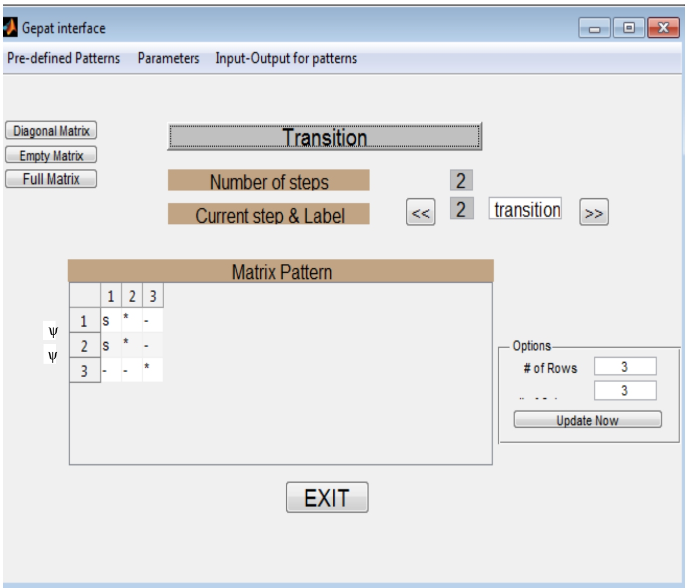
	1	2	3
1	y	-	*
2	-	y	*
3	-	-	*

# of Rows: 3
# of Columns: 3

The rows of the transition matrix specify the possible states occupied at time *t*, while the columns specify the possible states occupied at time *t*+1.

Thus, we specify the transition probabilities as follows:

$$\begin{array}{cc} & \begin{array}{ccc} \text{AS} & \text{AD} & \text{D} \end{array} \\ \begin{array}{c} \text{AS} \\ \text{AD} \\ \text{D} \end{array} & \begin{pmatrix} \psi & 1-\psi & 0 \\ \psi & 1-\psi & 0 \\ 0 & 0 & 1 \end{pmatrix} \end{array}$$



Number of steps: 2
Current step & Label: 2 transition

	1	2	3
1	s	*	-
2	s	*	-
3	-	-	*

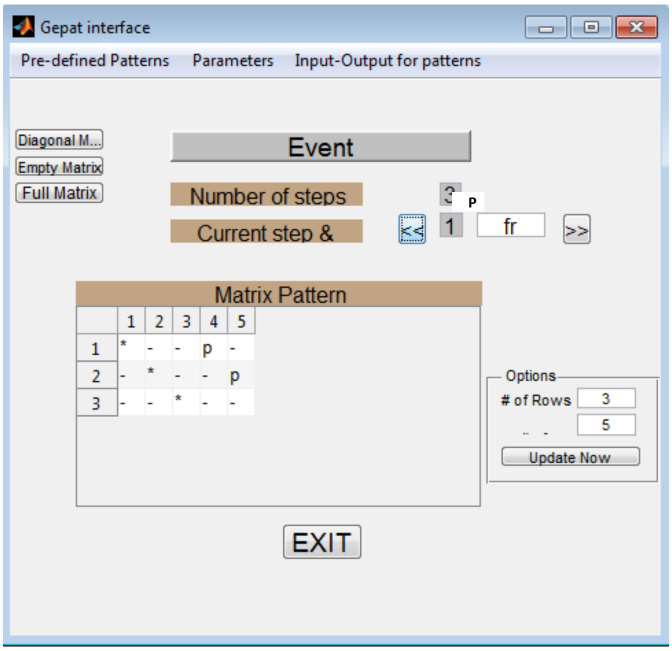
# of Rows: 3
3

The event matrices

We define three different event matrices (event probabilities are modelled in three steps; see Methods section for details). To increase the number of event matrices enter ‘3’ in the box right to the ‘Number of steps’. We called these matrices as [P] (focal bird recapture), [P2] (capture of the current partner), and [P3] (last-year partner recapture).

The matrix of **Step 1** describes the recapture probability of the focal individual (‘FC’ denotes the focal bird is captured, ‘FNc’ denotes a bird is not captured, superscript symbols after ‘FC’ and ‘FNc’ specify in which underlying state the focal bird is):

$$\begin{array}{c|ccccc}
 & FNc^{AS} & FNc^{AD} & FNc^{D} & FC^{AS} & FC^{AD} \\
AS & 1-p & 0 & 0 & p & 0 \\
AD & 0 & 1-p & 0 & 0 & p \\
D & 0 & 0 & 1 & 0 & 0
\end{array}$$



Number of steps: 3

Current step &: 1 P fr

Matrix Pattern

	1	2	3	4	5
1	*	-	-	p	-
2	-	*	-	-	p
3	-	-	*	-	-

Options

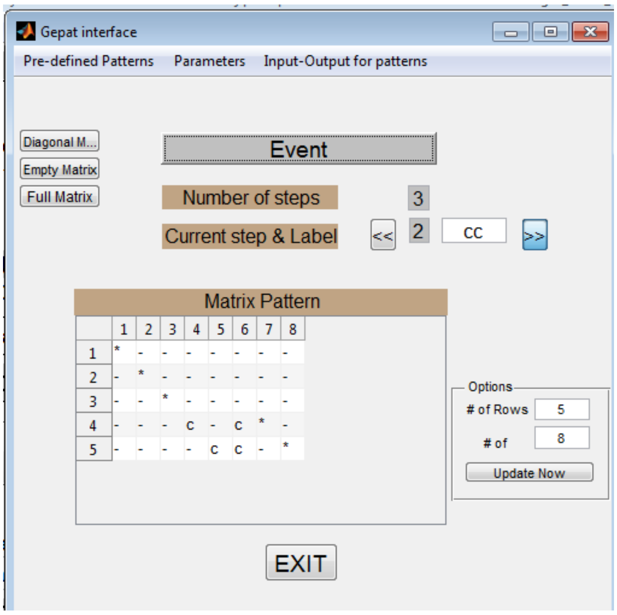
# of Rows: 3

.. -: 5

The matrix of **Step 2** describes the probability of capturing the focal individual’s current partner at *t* and knowing its identity in relation to the focal individual’s *t*-1 partner, conditional on the capture of the focal individual at *t*. The rows in this matrix correspond to the columns of the preceding matrix in **Step 1** (when modelling event probabilities, in each subsequent step the columns of the previous matrix become the rows of the next matrix). ‘PC’ denotes that current partner is captured; ‘PNc’ denotes that current partner is not captured; ‘PNn’ denotes current partner is captured but it is not known if it is the same or different to *t*-1 partner. Symbols in superscrips after ‘PC’, ‘PNc’, and ‘PNn’ specify in which underlying state a focal bird is.

$$
\begin{array}{cccccccc}
\mathrm{PNc}^{AS} & \mathrm{PNc}^{AD} & \mathrm{PNc}^{D} & \mathrm{PC}^{AS} & \mathrm{PC}^{AD} & \mathrm{PNn}^{AD,AS} & \mathrm{PNc}^{AS} & \mathrm{PNc}^{AD} \\
\end{array}
$$

$$
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & c & 0 & c & 1-\sum c & 0 \\
0 & 0 & 0 & 0 & c & c & 0 & 1-\sum c
\end{pmatrix}
$$



Number of steps: 3

Current step & Label: 2 CC

Matrix Pattern

	1	2	3	4	5	6	7	8
1	*	-	-	-	-	-	-	-
2	-	*	-	-	-	-	-	-
3	-	-	*	-	-	-	-	-
4	-	-	-	c	-	c	*	-
5	-	-	-	-	c	c	-	*

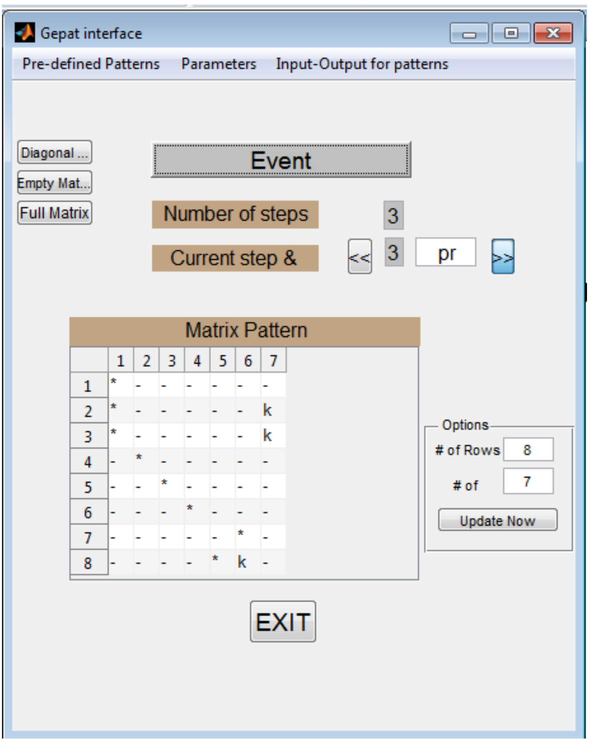
Options
# of Rows: 5
of: 8

P2

The matrix of **Step 3** describes the probability of capturing the focal individual’s *t*-1 partner if it was known in *t*-1) in the current year (*t*), incorporating information on its pairing status in the current year. Rows correspond to the columns of **Step 2**. The column numbers correspond to the event codes found in the capture histories.

$$
\begin{array}{ccccccc}
\mathbf{0} & \mathbf{1} & \mathbf{2} & \mathbf{3} & \mathbf{4} & \mathbf{5} & \mathbf{6} \\
\end{array}
$$

$$
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
1-l & 0 & 0 & 0 & 0 & 0 & l \\
1-l & 0 & 0 & 0 & 0 & 0 & l \\
0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 1-l & l & 0
\end{pmatrix}
$$



Number of steps: 3

Current step &: 3 pr

Matrix Pattern

	1	2	3	4	5	6	7
1	*	-	-	-	-	-	-
2	*	-	-	-	-	-	k
3	*	-	-	-	-	-	k
4	-	*	-	-	-	-	-
5	-	-	*	-	-	-	-
6	-	-	-	*	-	-	-
7	-	-	-	-	-	*	-
8	-	-	-	-	*	k	-

Options
# of Rows: 8
of: 7

P3

2.2 Specifying the model (defining shortcuts and using GEMACO interface)

To specify models, we have to define how parameters vary over time, groups, age classes, etc. To do this we use GEMACO interface to create a design matrix for each type of parameters.

First, we have to create a shortcut for age classes (yearling and adult birds). To do this click on the 'Shortcuts' button on the main E-SURGE screen. In our input file we have already defined explanatory variable 'Mgp' that can take values 'Ad' and 'Juv' depending on whether a bird was first caught as an adult or a yearling. This is shown in the 'Shortcuts' interface as:

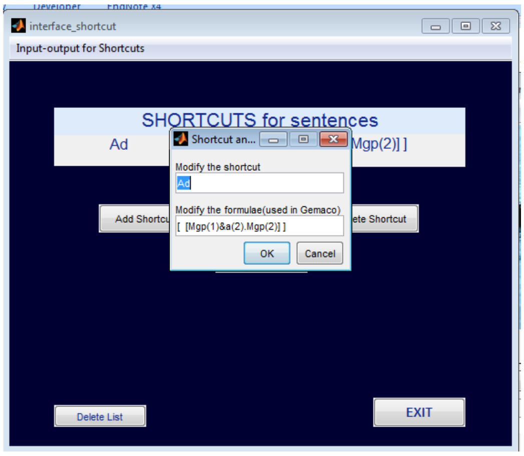
Mgp g(1,2)

1

Correspondence with initial covariate modalities

g(Ad,Juv)

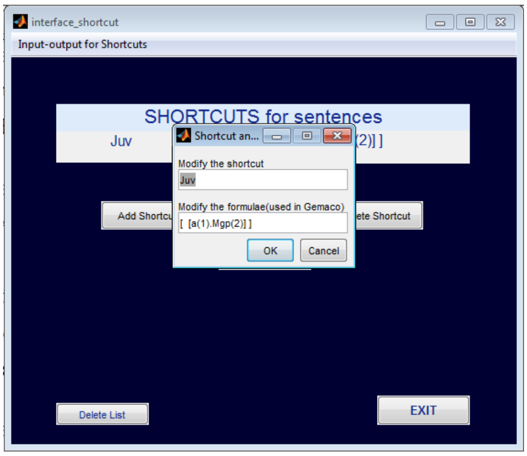
Next, click on the 'Add shortcut' indicator to create a new shortcut. Create two shortcuts 'Ad' and 'Juv' by typing a specific shortcut formula as shown below (for details on the meaning of GEMACO code please refer to the ESURGE manual, Choquet 2011):



Ad Mgp(2)]]

Modify the shortcut: Ad

Modify the formulae(used in Gemaco): [[Mgp(1)&a(2).Mgp(2)]]



Juv (2)]]

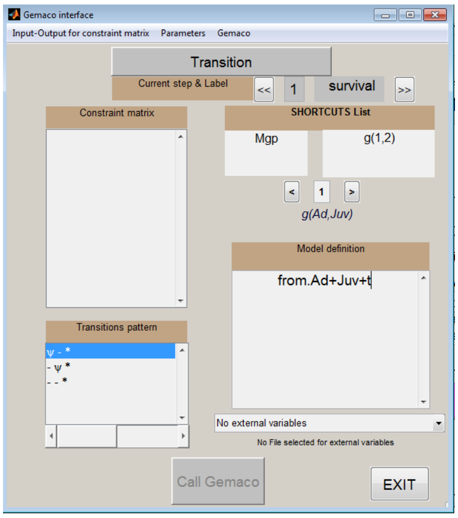
Modify the shortcut: Juv

Modify the formulae(used in Gemaco): [[a(1).Mgp(2)]]

When the shortcuts are defined, click the ‘EXIT’ button to exit the shortcut interface. Click the ‘GEMACO’ button to enter the GEMACO interface. In the GEMACO interface a syntax specifying variation of each parameter (independently of each other) is entered in the ‘Model definition’ window.

We constrain the initial state (at the IVFV stage we fix the probability of AD to be 1) to be constant over the study period, so leave the window blank and click on the ‘Initial state’ button to get at the ‘Transition’ screen.

To allow survival and transition probabilities to depend on both current state and age, and to be time varying, write the formula ‘**from.Ad+Juv+t**’ in the ‘Model definition’ box as shown below (shown for the first step, i.e. survival only, but the same GEMACO code is entered in both windows).



Current step & Label: 1 survival

SHORTCUTS List: Mgp g(1,2)

1 g(Ad,Juv)

Model definition: from.Ad+Juv+t

Transitions pattern:
ψ - *
- ψ *
- - *

No external variables

No File selected for external variables

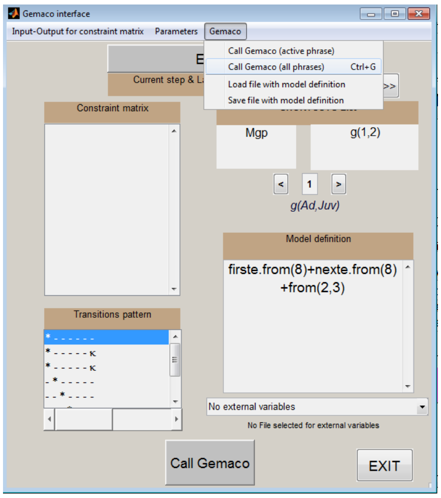
Click on the top ‘Transition’ button to progress to the ‘Event’ screen.

Multi-event models condition on the first encounter of each individual. This means that the event ‘not encountered’ becomes possible only after an individual has been caught. Thus, the event probabilities at the time of the first encounter must be treated separately from the subsequent event probabilities (and later fixed to one). In E-SURGE this is achieved by using the keywords ‘**firste**’ (stands for ‘first encounter’) and ‘**nexte**’ (‘next encounters’). To specify that event probabilities will vary with state and to allow for fixing the probability of the first encounter, write the following syntax into the ‘Model definition’ window: ‘**firste+nexte.to**’. We will fix the probability of the first encounter to be one at the later (IVFV) stage.

In the **Step 2** of the event probabilities we specify the ‘capture’ probability of the focal individual’s partner to depend on the current state. In our case, the capture probabilities in columns 4 and 5 of the event matrix represent true capture probabilities of the current partner, while the probabilities in the column 6 represent the combined probabilities of the capture of the current partner and the probability of knowing it’s relation to the last-year partner. To differentiate these, we write (4 5, 6) in the brackets after ‘**to**’. This forces the capture probabilities in the columns 4 and 5 to be equal and different form the capture probability in the column 6. The final syntax looks like this: ‘**firste.to(4 5,6)+nexte.to(4 5, 6)**.

Finally, in **Step 3** of the event probabilities we specify the probability of the recapture of the last-year partner. At the first capture of the focal individual the event 4 is not possible (i.e. probability of event 5, as the only other option, is 1) as the partner from the last year cannot be known for individuals captured for the first time, and consequently it cannot be captured in the current year. Thus, we need to allow for fixing the event 5 to equal 1 at the time of the first encounter later in the IVFV stage. To achieve this write the syntax ‘**firste.from(8)+nexte.from(8)+from(2,3)**’ in the ‘Model specification’ window.

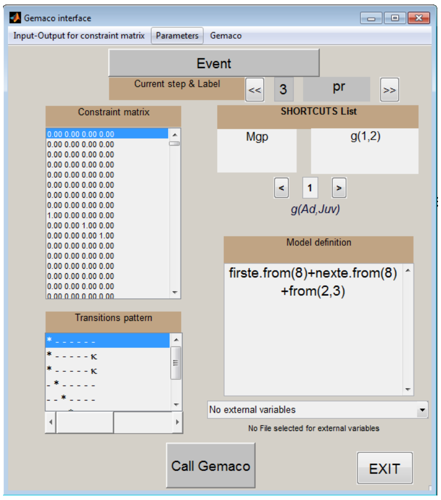
After specifying how the parameters of the initial state vector, and survival-transition and event matrices vary, we need to create the design matrices. This is done by clicking the ‘Gemaco’ item in the top menu and choosing ‘call GEMACO (all phrases)’ option:



```
firste.from(8)+nexte.from(8)
+from(2,3)
```

```
* - - - - - -
* - - - - - K
* - - - - - K
- * - - - - -
- - * - - - -
```

Now, all the model structures are specified and the design matrices appear in the left window of each screen of the GEMACO interface (shown below, only for the **Step 3**). To return to the main window click the EXIT button.



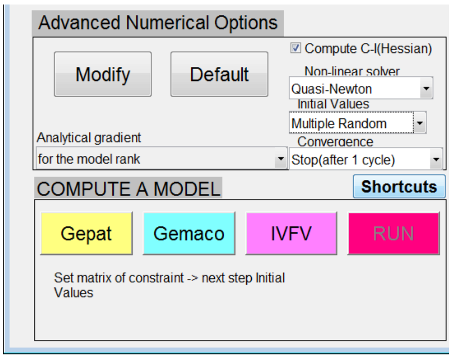
```
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
1.00 0.00 0.00 0.00
0.00 0.00 1.00 0.00
0.00 0.00 0.00 1.00
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
0.00 0.00 0.00 0.00
```

```
firste.from(8)+nexte.from(8)
+from(2,3)
```

```
* - - - - - -
* - - - - - K
* - - - - - K
- * - - - - -
- - * - - - -
```

2.3 Specifying the initial and fixed values using the IVFV interface

In the ‘Advanced Numerical Options’ part of the main window click the box left to ‘Compute C-I (Hessian)’ so that standard errors can be obtained. Choose ‘Multiple random’ option from the drop-down menu below the ‘Initial values’, and type the number of initial random values. This specifies the way the initial values of the optimisation procedure are generated and assists with model convergence issues.



☑ Compute C-I(Hessian)

Non-linear solver: Quasi-Newton

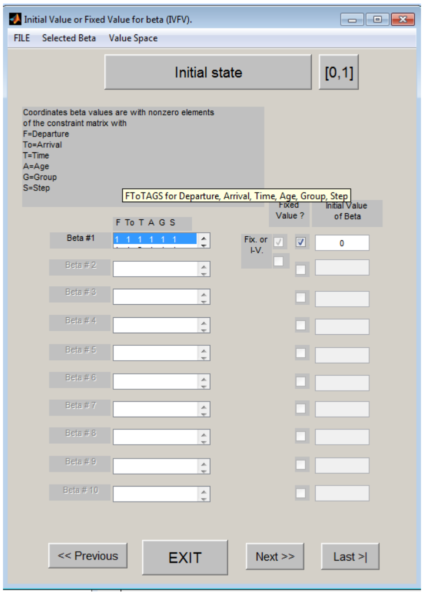
Initial Values: Multiple Random

Convergence: Stop(after 1 cycle)

Analytical gradient: for the model rank

Set matrix of constraint -> next step Initial Values

Press the IVFV button to enter the interface. For the initial state probabilities we have arbitrary chosen to fix the probability of ‘AD’ to be 1 (i.e. the probability of ‘AS’ is then equal zero).



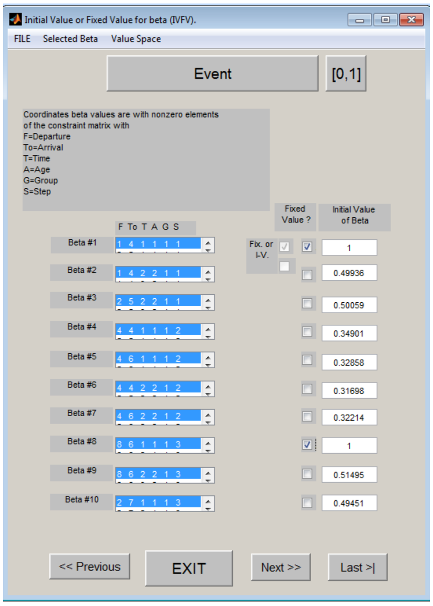
Coordinates beta values are with nonzero elements
of the constraint matrix with
F=Departure
To=Arrival
T=Time
A=Age
G=Group
S=Step

FToTAGS for Departure, Arrival, Time, Age, Group, Step

	F To T A G S		Fixed Value ?	Initial Value of Beta
Beta #1	1 1 1 1 1 1	Fix. or I-V.	☑	0

Click on the top ‘Initial state’ button to arrive at the ‘Transition’ screen. There is no need to fix the values for the transition probabilities, so leave the screen at its default state.

As discussed above, the probability of the first encounter of the focal individual equals 1, and the probability of capturing focal's last-year partner equals 0 in the current year (i.e. probability of not capturing it equals 1). To ensure this, fix the event probabilities as shown below:



Coordinates beta values are with nonzero elements
of the constraint matrix with
F=Departure
To=Arrival
T=Time
A=Age
G=Group
S=Step

	F To T A G S	Fixed Value ?	Initial Value of Beta
Beta #1	1 4 1 1 1 1	☑	1
Beta #2	1 4 2 2 1 1	☐	0.49936
Beta #3	2 5 2 2 1 1	☐	0.50059
Beta #4	4 4 1 1 1 2	☐	0.34901
Beta #5	4 6 1 1 1 2	☐	0.32858
Beta #6	4 4 2 2 1 2	☐	0.31698
Beta #7	4 6 2 2 1 2	☐	0.32214
Beta #8	8 6 1 1 1 3	☑	1
Beta #9	8 6 2 2 1 3	☐	0.51495
Beta #10	2 7 1 1 1 3	☐	0.49451

After specifying all the fixed values press the EXIT button. Press the RUN button of the main menu to run the model.

3. Additional procedures and codes to fit the pair fidelity model to combined great tit and blue tit capture histories (Chapter 4)

Here we outline additional actions to add to the procedures described in the Section 2 of this supplement, in order to fit the pair fidelity model to: combined dataset on the two populations of great tits (Wytham and Bagley) and on the two species (great and blue tits). If not stated differently, all the other steps are the same as in the Section 2. We use the best model selected in the female datasets (i.e. obtained after the full model selection), to demonstrate how to specify Population or Species dependent transition rates.

In the combined datasets, there is one additional explanatory variable in each dataset: '$COV:Pop' in the one combining the two populations of great tits (Wytham and Bagley populations); and '$COV:Sp' in the one combining the two species (great and blue tits). After you load the data, chose both covariates (i.e. Mgp and Pop; or Mgp and Sp) in the top left corner of the window that appears.

Specifying the model (defining shortcuts and using GEMACO interface)

In our input files we have already defined explanatory variables 'Mgp' that can take values 'Ad' and 'Juv'; 'Pop' that can take values 'Wytham' and 'Bagley'; and 'Sp' that can take values 'GT' and 'BT'. In the dataset combining the two populations of great tits, E-surge (automatically, according to alphabetical order) codes these as groups: 1 = Adult from Bagley; 2 = Juvenile from Bagley; 3= Adult from Wytham; 4 = Juvenile from Wytham. In the dataset combining the two species, E-surge codes groups as: 1 = Adult Blue tits; 2 = Juvenile Blue tits; 3 = Adult Great tits; 4 = Juvenile Great tits. We will use these codes (i.e. groups) to define parameter variation later (i.e. in the GEMACO).

In the GEMACO interface, to allow survival probabilities to depend on current state, age, to differ between resident adults (birds that have already bred at least once), and new adults (birds breeding for the first time a adults), and to be time varying, with the time variation following different pattern in the two populations, write the formula '**t.Pop+a(1).Age+a(2).from'** in the 'Model definition' box. To achieve the same parameter variation, but with species-specific time variation, enter the same syntax, replacing '**t.Pop**' with '**t.Sp'**.

Transition probabilities of the best model in the combined dataset on the two populations have the same parameterisation as the survival probability do, so write the syntax '**t.Pop+a(1).Age+a(2).from'** in the 'Model definition' box of the **Step 2** of the transition probabilities. In the combined dataset on the two species, to allow transition probabilities to depend on current state, age, differ between resident adults, and new adults, at different levels in the tow species, and time varying in great, but not blue tits, write the formula '**t.g(3 4)+Sp.[a(1).Age+a(2).from]'** in the 'Model definition' box. The syntax '**g(3 4)**' means that time variation will be applied to combined group ‘3’ and ‘4’, which are adult and juvenile great tits, respectively.

In the **Step1**of the event probabilities, to allow recapture probability of the focal individual to vary with state, species, and be time varying in Wytham great tits, but not in Bagley great tits, write ‘**firste+nexte.Pop.to+t.g(3 4)**’. Enter the same structure, but with **‘nexte.Sp.to**’ to allow the same parameter variation but according to species.

For both datasets, enter **‘firste.to(4 5,6).Sp+nexte.to(4 5,6).Sp’** for the **Step 2,** and ‘**firste.f(8).Sp+nexte.f(8).Sp+f(2,3).Sp’** for the **Step 3**.

4. Additional procedures and codes to fit the pair fidelity model to mute swans capture histories (Chapter 5)

Here we outline additional actions to add to the procedures described in the Section 2 of this supplement, in order to fit the pair fidelity model to data on breeding population of mute swans. If not stated differently, all the other steps are the same as in the Section 2. We use the best model selected in the female datasets (i.e. obtained after the full model selection) from the model selection on the full dataset.

In the swan dataset, the covariate ‘$COV:Mgp’ can take values from 2 to 9, as these is the real age a swan was captured breeding for the first time (with 9 representing birds 9 or more years old). In the ‘Data’ click the button ‘Modify’ to change the number of states to 3, and the number of age classes to 15.

Specifying the model (defining shortcuts and using GEMACO interface)

In our input files we have already defined explanatory variables ‘Mgp’ that can take values from ‘2’ to ‘9’. E-surge (automatically, according to alphabetical order) codes these as groups from ‘1’ to ‘9’ (these correspond to the original groups from ‘2’ to ‘9’). In this step, do not define the Shortcut ‘Age’ (as we did in the modelling on great tits). We will use these existing codes (i.e. groups) to define parameter variation later (i.e. in the GEMACO).

In the GEMACO interface, we want to allow survival probabilities to depend on chorological age (birds old 2 to 8 year, and older), current state, and to be time varying. In E-surge, it is easy to allow individual to 'age' counting from the time when they were first captured (i.e. always starting from 1). However, to code the real aging, given that individuals are captured for the first time at different chronological age, and that this chronological age has to change in each subsequent breeding season, is more complicated. Thus, to allow the variation according to the real age (and to incorporate the need that state dependence in survival rates does not apply to the individuals captured for the first time), write the formula **'[g(1).a(2:7)&g(2).a(2:6)&g(3).a(2:5)&g(4).a(2:4)&g(5).a(2:3)&g(6).a(2)+g(1).a(8:15)&g(2).a(7:15)&g(3).a(6:15)&g(4).a(5:15)&g(5).a(4:15)&g(6).a(3:15)&g(7).a(2:15)&g(8).a(2:15)].f+a(1).g(1)+a(1).g(2:7)+a(1).g(8)+t '** in the 'Model definition' box of the **Step 1** of the 'Transition' window.

To allow transition (i.e. fidelity) probabilities to depend on the time since the first capture (i.e. to be different between the 1st and 2nd breeding season, and later breeding season), write the formula '**a(1)+a(2:15).f+t'** in the 'Model definition' box of the **Step 2** of the 'Transition' window.

In the **Step1**of the event probabilities, to allow recapture probability of the focal individual to vary with state, age since first capture (i.e. to be different between 1st and 5th breeding season, and later), and be time varying in, write '**firste+nexte.a(1:5, 6:16).to+t**'. The other two steps are the same as in the great tits.

CHAPTER 4

Evidence of a link between survival and pair fidelity across multiple tit populations

Evidence of a link between survival and pair fidelity across multiple tit populations

Antica Culina, Shelly Lachish, and Ben C. Sheldon

ABSTRACT

1. Although they have the potential to strongly influence individual fitness and the dynamics and productivity of populations, the survival consequences of pairing outcomes and the influence of current pairing outcomes on those in the future have rarely been addressed. Previously, we have shown that pair fidelity increases both survival and future fidelity in a population of great tits (*Parus major*).

2. The aim of the current study was to explore the generality of our previous findings by evaluating the influence of current paring outcomes on survival and on future pairing outcomes in two different species, in different populations, and according to age and sex.

3. We addressed our aims within a multievent capture-mark-recapture (MECMR) statistical framework, which accounts for differences in recapture rates and uncertainty in the assignment of pair status (i.e. whether an individual is breeding with the same partner or not). We applied the framework to breeding records of two great tit populations of one blue tit (*Cyanistes caeruleus*) population.

4. We detected survival benefits (i.e. increased survival) of pair fidelity in all three populations. These were similar in both great tit populations, but higher for male great tits than for male blue tits. We found that an age-dependence in the rate of fidelity was shared between different populations and species, but did not detect any influence of current pair status on future pair status.

5. Our study highlights the importance of considering survival when studying the fitness benefits of pair fidelity. Some of the differences in fidelity rates and survival benefits of fidelity are likely the result of long-term and short-term population factors. We advocate the use of the MECMR framework used here for further exploration of these differences.

INTRODUCTION

Birds are generally socially monogamous (Bennett and Owens 2002). However, both within species and among species they show variable rates of pair bond maintenance between subsequent breeding seasons (i.e. pair fidelity rates). Individuals that survive between two subsequent breeding seasons may either re-pair with the previous partner or change partner. Partner change can happen either because the previous partner died (i.e. widowing) or because of 'divorce' (when the previous partner is still alive). The fitness consequences of these pairing outcomes, along with variation in demographic and environmental factors, will influence pair fidelity rates at the individual, population and species level. Knowledge of the fitness consequences and drivers of differences in pair fidelity rates is important for understanding the evolution of long-term partnerships and monogamy (Reichard and Boesch 2003, Shuster and Wade 2003), mate choice (Diamond 1987, Black 1996), and population productivity and dynamics (Sugg et al. 1996, Berec and Boukal 2004, Maxin and Berec 2010).

A common approach to understanding the fitness correlates of fidelity is to compare the breeding success of pairs in different pairing outcomes. Breeding success often increases as a consequence of repeated breeding with the same individual (e.g. Perrins and McCleery 1985, Wiktander et al. 2001, Pampus et al. 2005), but in some cases partner change can also lead to an increase in breeding success (reviewed by Culina et al. 2014: Chapter 2). At the species and population level, drivers of pair fidelity are often addressed by correlating pair fidelity rates to species- and population-specific life-history (Rowley 1983, Jouvetin and Bried 2001, Bried et al. 2003, Jeschke and Kokko 2008), ecological and demographic factors (Ens et al. 1993, Dhondt et al. 1996, Bried and Jouventin 1999, Maness and Anderson 2007), or to classes of individuals sharing a certain trait of interest (e.g. commonly age classes, Pampus et al. 2005, Llambias et al. 2008).

However, studies of the fitness correlates and consequences of pair fidelity generally fail to acknowledge survival as a possible fitness consequence of pairing outcomes. They also do not account for biases in the estimation of fidelity rates, which can easily lead to flawed conclusions. Pair fidelity can affect survival through several mechanisms. Faithful individuals might be better able to acquire resources in winter (Black 1996, Black 2007), or better coordinate parental duties (Hall 1999, Naves et al. 2007) leading to better body condition at the beginning of winter, and higher winter survival. To our knowledge only two studies have shown that pair status can influence winter survival. Nicolai et al. (2012) found that female black brant geese (*Branta bernicla nigricans*) whose partners died during winter suffered reduced winter survival, but not reduced breeding success, if they survived to breed. Meanwhile, in a previous study we showed that male and female great tits (*Parus major*) that breed with a different partner than in the previous season had a lower survival rate to the next season compared with faithful birds (Culina et al. 2013: Chapter 3). The paucity of studies examining survival-fidelity correlates is in part caused by the inability to distinguish between individuals that have died and those that simply were not captured. A further complication is that recapture probability might also be linked to fidelity: for instance, unpaired individuals might range more widely which, depending on the method used to collect data, might either increase or decrease their likelihood of observation or capture compared to paired individuals. To date, almost all research on the causes and consequences of pair fidelity has been based on the recapture of breeders in subsequent breeding seasons to determine pair status (i.e., whether individuals are breeding with the same partner as in the last season, or not). This method requires that both an individual’s current and previous partners are known and captured. However, in most studies of wild populations, recapture rates are lower than one, sometimes substantially so (Archaux et al. 2012), and are also often demographically biased (Crespin et al. 2008, Carter et al. 2012, Culina et al. 2013: Chapter 3). Consequently, assessments of pair status are often likely to be inaccurate and biased. Finally, the inability to assign pair status with certainty complicates the exploration of how current pairing outcomes might influence future ones (St. Clair et al. 1999, Culina et al. 2013: Chapter 3). This possibility is especially interesting to study from the perspective of carry-over effects of pairing outcomes: pairing outcomes in one year might influence fitness beyond the immediate breeding season.

The challenges of the imperfect observation process and the uncertainty in assigning pair status can be overcome by modelling fidelity and survival in a unified statistical framework using multievent capture-mark-recapture (MECMR) modelling. MECMR models (Pradel 2005) use the same principle as multistate capture-mark-recapture models (Arnason 1972, 1973, Hestbeck et al. 1991) to estimate transition rates of individuals among different 'states' (e.g., reproductive status, breeding locations), and to impose different constraints on these transitions (e.g. state- and time- dependence, individual covariates). In addition to this, MECMR models incorporate uncertainty in state assignment by relating the unknown or partly observable states to observations of captured individuals (termed 'events') through a series of conditional probabilities (Pradel et al. 2008).

In this study, we apply a MECMR modelling framework of pair fidelity (Culina et al. 2013: Chapter 3) that incorporates differences in recapture rates, and uncertainty in the assignment of a pair status, to test for the survival benefits of fidelity, and to explore several predictions of drivers of the differences in pair fidelity. We carried out these analyses making comparisons between populations and between individuals within those populations using long-term data on two adjacent populations of great tits (Wytham Woods and Bagley Wood, near Oxford, UK) and a population of blue tits (Wytham Woods). Specifically, we aimed to answer the following four questions.

(1) Are apparent survival benefits of pair fidelity present, and if so, to what extent are these species- and population-specific?

(2) Are annual variations in fidelity rates more similar within species or within populations, and hence, is variation in fidelity rates driven by local-scale or large-scale effects?

(3) Does past breeding status influence the likelihood of future breeding outcome, and to what extent are these patterns common across species?

(4) Are age-dependent effects on fidelity rates consistent across populations and species?

METHODS AND DATASETS

Multievent modelling framework

In MECMR models (Pradel 2005) individuals occupy one (exclusive) state at each capture occasion and can move between a discrete number of mutually exclusive states between two subsequent capture occasions. However, because it is not always possible to unambiguously allocate an individual to a state, what is observed are 'events' rather than states. Each event relates to one or more states through a series of conditional probabilities (Pradel et al. 2008, Choquet et al. 2009b) and provides information about the real underlying state of an individual. In this study we use a specific MECMR model of pair fidelity we have previously developed (Culina et al. 2013: Chapter 3). At each breeding season (which is the capture occasion) an individual can be in one of three mutually exclusive states (we term these 'pair status'):

(1) Alive and breeding with its partner from the previous year ('AS');

(2) Alive and breeding with a different partner to the previous year ('AD'); and

(3) 'Dead'.

Individuals can move from state to state between two consecutive breeding seasons (with ‘Dead’ being an absorbing state). The movement is modelled in two steps: survival and then transition (i.e. ‘fidelity’, which is conditional on survival). Capture histories of individuals consist of event codes (seven possible events, coded from 0 to 6, see below) with each code representing an event that is observed for each individual at each capture occasion (i.e. each breeding season). The events incorporate information on the capture of the focal individual, information on the capture of its current partner, and information on its previous partner (see Fig 1, Culina et al. 2013: Chapter 3). These events (and the corresponding possible underlying states of the focal individual, given in brackets) are:

- **event 0** = the focal individual was not captured at current breeding season (*t*). Its partner from the *t*-1 was either not captured at *t-1* or *t*, or was captured breeding at *t* at an active nest with an unknown partner (‘AS’, ‘AD’, ‘Dead’);
- **event 1** = the focal individual was captured at *t* and was breeding with its partner from *t-1* (‘AS’);
- **event 2** = the focal individual was captured at *t* and was breeding with a different partner to that from *t-1* (‘AD’);
- **event 3** = the focal individual was captured at *t* but it was not known whether its current partner (which was captured) was the same as that from *t-1* (‘AS’, ‘AD’);
- **event 4** = the focal individual was captured at *t*. Its current partner was not captured and its partner from *t-1* was captured at *t* at a different nest (thus, was not breeding with the focal individual; ‘AD’);
- **event 5** = the focal individual was captured at *t*. Its current partner was not captured, and its partner from *t-1* was either not captured in *t* or was not known in *t-1* (‘AS’, ‘AD’);

- **event 6** = the focal individual was not captured at *t* (hence its *t* partner was unknown). Its partner from *t-1* was captured breeding with another individual at *t* (‘AS’, ‘AD’, ‘Dead’).

In line with the framework described above, the model uses three types of parameters: (1) initial state probabilities (the probability of an individual being in a certain state when captured for the first time); (2) transition probabilities: composed of survival probability and the between-state transition probabilities (conditional on survival); and (3) event probabilities (conditional on the underlying state) composed of: recapture probabilities of the focal individual, capture probabilities of its current partner, and recapture probabilities of the previous year’s partner. All of these probabilities are represented in the vector of the initial state probability, survival matrix, transition matrix, and three event matrices. By imposing different constraints on the variation of the parameters in the matrices, it is possible to test among different hypothesis on the factors influencing the probabilities. For more details see Culina et al. (2013), and the Appendix of Chapter 3.

Study populations

We used records of breeding pairs of great and blue tits in Wytham Woods (51° 46’ N, 1° 19’ W), and of great tits in nearby Bagley Wood (51° 42’ N, 1° 15’ W). Both sites are mixed-species, predominantly deciduous, forest, where a large proportion of the breeding birds nest in next boxes. Wytham great tits have been studied using the standardized breeding protocol since the 1960s (Perrins 1965, Perrins 1979, Gosler 1993); however, an intensive individual-based study of the blue tit at this site has been more discontinuous. For the purposes of the current work, we used data that were collected annually using standardised methods since 2001 (e.g. see Wood et al. 2007, Lachish et al. 2011). Great tits in Bagley Wood have been studied since 2007, using similar methods to those in Wytham (see Evans and Sheldon 2012 for more details of this population). Each bird known to be born in the woods was ringed with a uniquely numbered BTO ring as a nestling. In addition, immigrants were either ringed when captured breeding for the first time (i.e. during the breeding season) or during extensive winter catching sessions. The age of breeders can be determined either from the year they were ringed as chicks (locally born birds), or from plumage characteristics for immigrants (according to Svensson 1992). In the breeding season all active nests in nestboxes were identified by regular inspections, and by attempts to capture parents while they feed their chicks (between day 6 and 14 of the nestling phase). In most cases this provided the identities of both parents, but in some cases only the female or (less often) only the male was captured, while the other parent remained unknown. The number of breeding attempts where both parents, only female or only male was identified, number of capture histories for each sex of blue and great tits in Wytham Woods, and great tits in Bagley Wood, and the years covered in our analysis are provided in Table 1. Because the majority of individuals have short life-spans and because it was not always possible to know the exact age of immigrants, we assigned age either as 'first year' (birds captured breeding a year after they were born), or 'adult' (2+years old).

Table 1. Sample sizes and time periods for which data on great tits and blue tits breeding in Wytham Woods, and great tits breeding in Bagley Wood were used to model survival benefits of pair fidelity and fidelity rate correlates. Numbers of capture histories are given for females and males separately. Each capture history corresponds to one individual.

Species/Population (years covered)	N of breeding attempts (proportion in the overall number of breeding attempts)				N of capture histories	
	Both parents captured	Only F captured	Only M captured	Overall	Females	Males
Great tits/Wytham (2001-2012)	3165 (0.80)	693 (0.18)	85 (0.02)	3943	2437	2117
Blue tits/Wytham (2001-2012)	2764 (0.72)	843 (0.22)	218 (0.06)	3825	2704	2206
Great tits/Bagley (2007-2013)	935 (0.84)	155 (0.14)	28 (0.02)	1118	712	655

Model covariates and model selection process

To avoid problems of non-independence between males and females from the same population, we modelled the sexes in separate analyses. This led to 6 different sets of capture histories: male great tits in Wytham Woods (2001 to 2012), female great tits in Wytham Woods (2001 to 2012), male blue tits in Wytham Woods (2001 to 2012), female blue tits in Wytham Woods (2001 to 2012), male great tits in Bagley Wood (2007 to 2013) and female great tits in Bagley Wood (2007 to 2013). The great tit data from Wytham overlap with those for which similar analyses were reported in Culina et al. (2013), where we analysed data from 1980 to 2009 (here we use data from 2001 to 2012). We repeated the analyses for these data here because (i) we wished to make direct comparisons and (ii) we then sought to combine datasets. We also combine these datasets in two ways to investigate population and species difference in fidelity rates and survival-fidelity correlates. We obtained two 'Population Datasets' by combining the datasets for great tits at Wytham and Bagley for each sex separately (2007 to 2012). We obtained two 'Species Datasets' by combining the datasets for blue and great tits at Wytham, for each sex separately (2001 to 2012). We conducted analyses on both separate and combined datasets because combining two populations in the same analysis also requires that the new dataset is adjusted to the length of the monitoring period of the population with the shorter monitoring, and this may cause some patterns (that can be captured in the longer-term dataset) to be overlooked.

Currently, a specific goodness-of-fit (GOF) test for MECMR models is not available. Thus, we assessed the fit of the single state Cormack-Jolly-Seber (CJS) model to our data. The CJS model allows for full time variation and no age effect in survival and recapture rates (Choquet et al. 2009a), and assumes that all animals present in the same capture occasion have equal future survival and recapture probabilities regardless of the capture in the current capture occasion. We tested the assumptions using program U-CARE (Choquet 2005, Choquet et al. 2009a) in each of the separate datasets.

After checking the general mark-recapture assumptions, we proceeded with the model selection. We first determined the way that recapture, survival and fidelity vary within each of the six Separate Datasets. In this first set of analyses we considered time and state-dependence in recapture rates, time-, state- and age-dependence in survival and fidelity rates, and several possible combinations of these (see Table 2 for the list of covariates and their combinations for each of the parameters). We restricted the variation by state to adult birds only, as birds breeding for the first time cannot be considered as faithful or partner changed. When testing for the influence of age, we also tested whether there was any difference between individuals that were adults when first observed breeding ('New adults') and adults that had previously bred, either as first years, or as adults ('Resident adults').

We applied a 3-stage model selection (Grosbois and Tavecchia 2003) on each dataset. In the first step, we selected the best recapture model amongst the set of models with different constraints on the variation in recapture rates, but the same (and fully parameterised) covariates of survival and fidelity rates. In the second step, we modelled survival rates while keeping recapture rates parameterised according to the best recapture model (or models, if two or more recapture models gained the best support) selected in the first step, and fully parameterised fidelity rates. In the third step, we modelled the fidelity rates while keeping the structure of the best-supported model (or set of models) identified in the first two steps. We based model selection on the AIC values (Anderson and Burnham 2002): if the difference in the AIC values between two models was larger than 3, we considered the model with the lower value as having better support. If the difference was less than 3, we considered that models gained equal support. The list of model structures that were compared is given in Supplementary Tables S1 to S6.

Table 2. Covariates (and their combinations) considered in the MECMR modelling of recapture, survival, and fidelity rates in blue and great tits. t = time; state = pair status (pair faithful or partner changed); 1y = 'first years', birds captured breeding a year after they were born; Ad = all adults; AdN = adults that are recorded breeding for the first time when already adults; AdR= resident adults that have previously bred, either as first years, or adults; + = additive effect of covariates; × = interactive effect of covariates.

parameter	main covariates	structure of the models contrasted
recapture	t state	state t state + t no covariates
survival	t state 1y + Ad 1y + AdN + AdR	time 1y + Ad + t 1y + AdN + AdR × state + t 1y + Ad × state + t 1y + AdN + AdR + t
fidelity	t state 1y + Ad 1y + AdN + AdR	t 1y + Ad + (t) 1y + AdN+ AdR × state + (t) 1y + Ad × state + (t) 1y+ AdN + AdR + (t)

In our second set of analyses, we quantified population- and species-specific survival benefits of pair fidelity and variation in pair fidelity rates by using the Population Datasets and the Species Datasets. Specifically, we tested for species and population differences in the (i) survival benefits of pair fidelity, (ii) the overall (mean) rates of pair fidelity, (iii) temporal patterns of fidelity rates, and (iv) age and state-dependence of fidelity rates. First, we ran the 3-stage model selection (organised in three steps, i.e., selecting the best recapture, survival, and transition model) using basic model structure (i.e., variation in parameters) as obtained from the first set of model selection on the separate datasets, with 'species' or 'population' added as an interactive or additive factor to each particular model parameter. In addition, to specifically test whether survival benefits of pair fidelity are species- or population-specific we compared the following two sets of survival model structures:

- **set 1:** a) first years + New adults + Resident adults × state
  b) [first years + New adults + Resident adults × state] × species (or population)
  c) first years + New adults + Resident adults x state + species (or population)
- **set 2:** a) adults × state
  b) adults × state × species (or population).

Similarly, to test if there was any difference in the influence of the current pairing state on the future one we compared the models with the structure as in the **set 1** and the **set 2,** but in the fidelity part of the model.

Finally, to test specifically whether the overall level of fidelity rates differed between species or populations, and whether the time variation in fidelity rates was different between species and between populations, we compared models in the following two sets of models for variation in fidelity rates:

- **set 3** a) no time variation
  b) no time variation + species (or population)
- **set 4** a) time
  b) time + species (or population)
  c) time × species (or population).

A list of all models we contrasted is given in Supplementary Tables S7 to S10. We provide the details on the implementation of the models in the program E-SURGE (Choquet 2005, Choquet et al. 2009b) in the Appendix of Chapter 3 (Sections 1 to 3). Estimates of the rates we present in Results section are given as means with the 95% CI.

RESULTS

The results of the GOF tests did not reveal any detectable lack of fit of the CJS to the data in any of the separate datasets, and there was no evidence of overdispersion. In female great tits in Wytham Woods, results of the global test returned χ^2 =28.20, with df = 30, and P = 0.56 (the corresponding ĉ = 0.94). In male great tits in Wytham Woods results of the global test returned χ^2 =29.23, with df = 32, and P = 0.61 (the corresponding ĉ = 0.91). In female great tits in Wytham Woods results of the global test returned χ^2 =29.23, with df = 32, and P = 0.61 (the corresponding ĉ = 0.91). In female great tits in Bagley results of the global test returned χ^2 =22.59, with df = 14, and P = 0.07 (the corresponding ĉ = 1.61). In male great tits in Bagley results of the global test returned χ^2 =12.70, with df = 13, and P = 0.47 (the corresponding ĉ = 0.98). In female blue tits in Wytham, results of the global test returned χ^2 =20.35, with df = 34, and P = 0.97 (the corresponding ĉ = 0.60). In male blue tits in Wytham Woods results of the global test returned χ^2 =26.63, with df = 36, and P = 0.87 (the corresponding ĉ = 0.74).

Model selection on the separate datasets

The best-supported models for female (Supplementary Table S1), and male (Supplementary Table S2) great tits in Wytham Woods included: (i) time-varying and pair status-dependent recapture rates; (ii) time-varying, age- and pair status-dependent survival rates, that differed between new and resident adults; (iii) time-varying and age-dependent fidelity rates in both sexes, that differed between new and resident males, but not between new and resident females. There was no clear support for pair status-dependent future fidelity rates (i.e. same support for models with and without pair status-dependence in fidelity rates). Parameter estimates obtained from the best models showed that recapture was slightly lower for females (0.67, 0.64-0.70) and males (0.54, 0.51-0.57) breeding with a different partner than for faithful females (0.70, 0.65-0.74) and males (0.64, 0.59-0.70). As predicted, survival to the next breeding season was almost twice as high for faithful females (0.58, 0.53-0.63) and faithful males (0.62, 0.56-0.68) than for females (0.33, 0.30-0.36) and males (0.35, 0.32-0.38) that had changed partner. Fidelity rates of males that were first captured breeding as adults were much lower (0.18, 0.12-0.25) than fidelity rates of first years (0.27, 0.18-0.37) and other adult males (0.28, 0.20-0.38). Female first years had lower fidelity rates than adults did (first years: 0.25, 0.19-0.30; adults: 0.30; 0.23-0.39).

The best-supported models for female (Supplementary Table S3), and male (Supplementary Table S4) great tits in Bagley Wood included: (i) time constant and state-dependent recapture rates; (ii) time-varying, age- and pair status-dependent survival, that differed between new and resident adults; (iii) time-varying fidelity rates in both sexes, and age-dependence in fidelity of females. Fidelity models with pair status, with resident or new adults, and with age (in males) gained the same support as the models without these variables. Recapture rates were higher for faithful females (0.80, 0.70-0.87) and males (estimated near 1), and lower for females (0.55, 0.49-0.61), and males (0.40, 0.34-0.47) that had changed partners. Survival was around 30% higher in faithful females (0.45, 0.36-0.53) than in those females that changed partner (0.29, 0.23-0.34). Survival was also around 30% higher in faithful males (0.47, 0.35-0.59) than in males that changed partner (0.32, 0.27-0.38).

Model selection on the female (Supplementary Table S5) and male (Supplementary Table S6) blue tits in Wytham gave the best support to: (i) time-constant recapture rates, and the same support for pair status-dependent and independent recapture; (ii) time-varying, age- and state-dependent survival, that differed between new and resident adults; (iii) time-constant and age-dependent fidelity rates in males. In the male dataset, models with pair status, and with resident vs. new adults-dependent fidelity gained similar support as the models without these variables. In female dataset all fidelity models gained similar support. Survival estimates (which were similar across the models with different recapture and fidelity structures) showed that faithful females had almost twice as high survival (0.48, 0.41-0.55) compared to those females that changed partner (0.26, 0.22-0.30). Survival benefits of pair fidelity were also evident in males (faithful: 0.51, 0.43-0.58; changed: 0.31, 0.27-0.36). Adult males showed higher rates of pair fidelity (0.32, 0.27-0.38) than did first year breeders (0.20, 0.17-0.25).

Modelling survival benefits of pair fidelity and pair fidelity rates in two populations of great tits

Neither the main model selection (after selecting for the best recapture model) on survival rates, nor the specific survival hypotheses tests detected any difference in survival benefits of pair fidelity in different populations of great tits in females (Supplementary Table S7) and males (Supplementary Table S8). In other words the difference between survival of birds that had changed partner and those that were faithful was similar in the two populations. As expected, survival showed population-specific time variation, but the overall survival rates for different classes of individuals were strikingly similar between the populations (Figs 1A&B).

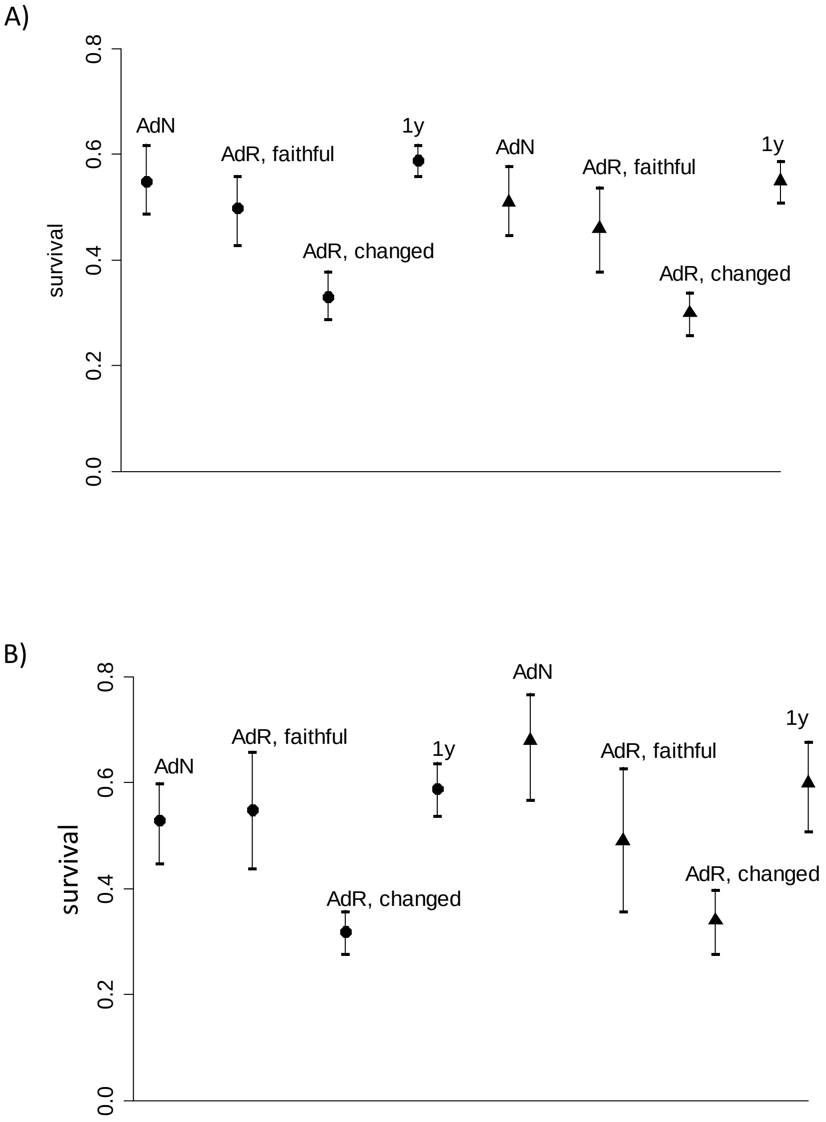


Figure 1. The overall annual survival rates through study period, 2007-2012 for A) female and B) male great tits in two populations of great tits (Wytham Woods = circles; and Bagley Wood = triangles), according to a pair status (faithful or partner changed, this only applies to adult birds that had bred at least once before), and whether they are 1st year breeders, adults captured for the first time as adults (AdN), or adults that were already previously captured breeding (AdR).

Model selection on the fidelity rates did not detect any difference in the overall (i.e. average) rates of fidelity at the population level. Interestingly, while time variation of fidelity rates in females was population-specific (Fig 2A), this was not the case for males: rates of male pair fidelity showed same temporal pattern in both populations (Fig 2B). Finally, model selection (both the general model selection, and specific tests) did not give support to any population-specific difference in fidelity rates between first years and adults, or between adults of different pair status (Supplementary Tables S7&8).

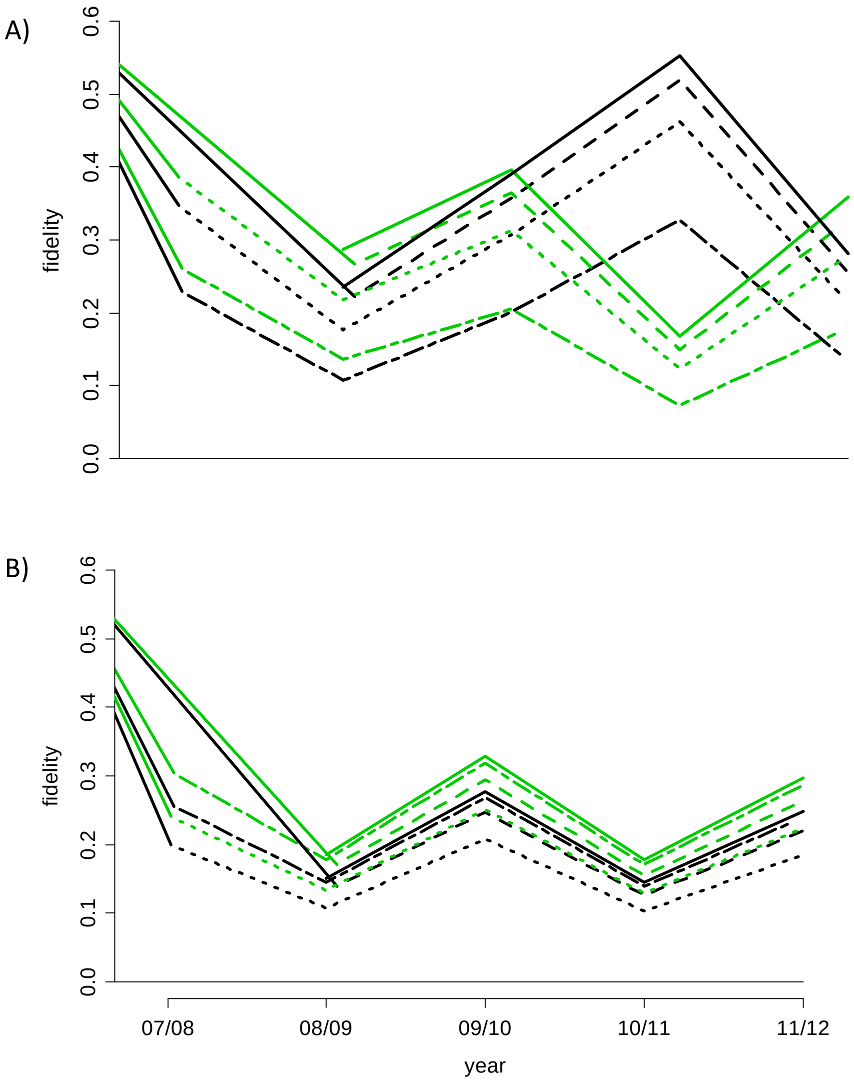


Figure 2. Pair fidelity rates of A) female and B) male great tits in two populations (Wytham Woods = black; and Bagley Wood = green), for 1st year breeders (dotted line), birds captured for the first time as adults (unevenly broke line), and the pair status of birds that had bred at least once before (faithful = full line, or partner changed = evenly broken line). Note that the between the first two seasons of data collection (i.e. 2007 and 2008) fidelity rates could only be estimated for the first two groups. The estimation of the fidelity rates of birds that have bred at least once was only possible starting from the 2008 breeding season.

Modelling survival benefits of pair fidelity and pair fidelity rates in two sympatric populations

Model selection on the survival rates of both sexes revealed species-specific time variation in survival (Supplementary Tables S9&10, Figs 3A&B). The species-specific effect on the benefits of pair fidelity was supported in the specific test for the influence of the species on the level survival is affected by pair fidelity for males (Supplementary Table S10); the difference in the survival between faithful and partner changed males was more pronounced in great tit males. Interestingly, this was driven by faithful male great tits having higher survival than faithful male blue tits (great tits: 0.61, 0.56-0.66; blue tits: 0.45, 0.39-0.51), while the survival of males that changed partners was similar (great tits: 0.33, 0.30-0.37; blue tits: 0.33, 0.29-0.38). The result indicates that benefits of staying with the same partner might be higher for male great tits than for male blue tits (Fig 3B). There was no support for a similar pattern in females (Supplementary Table S9). Contrary to our prediction, the overall fidelity rates in both females and males were found to be similar in both species. However, although the average fidelity rates were similar, fidelity rates varied with time in great tits, but were time constant in blue tits. There was no support for the difference in fidelity rates between adult and first year females and adult and first year males being different in different species (Supplementary Tables S9&10).

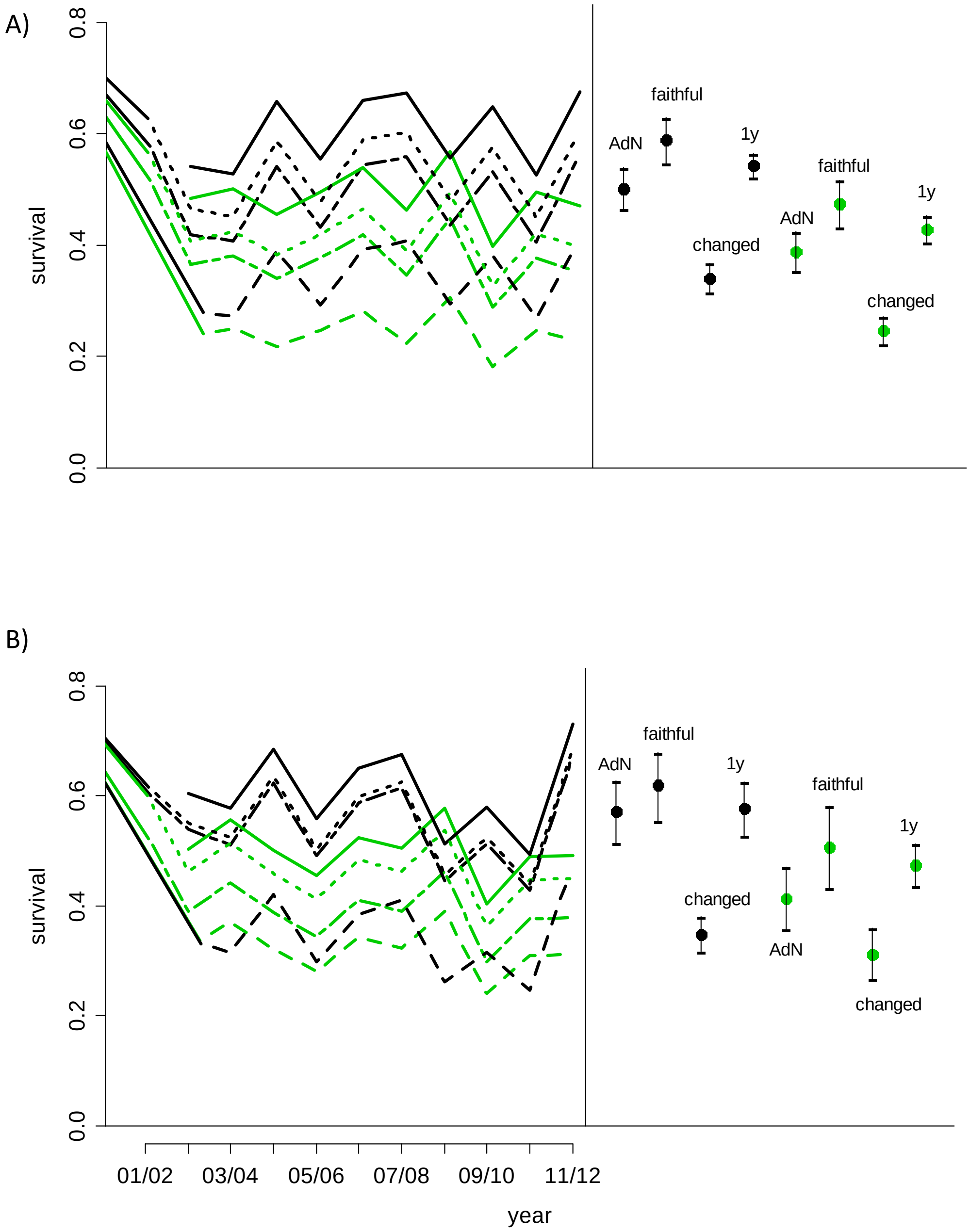


Figure 3. Survival of A) female and B) male great (black lines) and blue tits (green lines) in Wytham Woods for 1st year breeders (dotted line), birds captured for the first time as adults (unevenly broke line), and the pair status of birds that had bred at least once before (faithful = full line, or partner changed = evenly broken line). Note that the between the first two seasons of data collection (i.e. 2001 and 2002) survival rates could only be estimated for the first two groups. The estimation of the fidelity rates of birds that have bred at least once was only possible starting from the 2002 breeding season.

DISCUSSION

Survival benefits of pair fidelity

Our analyses revealed that pair fidelity and partner change are linked to survival in two species (great and blue tits), suggesting this might be a widespread phenomenon. This finding highlights the importance of studying survival when addressing the fitness consequences of paring outcomes because, as our work reveals, pairing outcomes impact fitness not only through the breeding success of established pairs, but also through survival. This possibility has rarely been considered in previous studies of the adaptive value of pairing decisions. Differences in survival linked to pairing choices might be especially important in species where pair members overwinter together, and where associating with a partner might confer higher rank in a competitive winter environment (Ekman 1990, Lemmon et al. 1997). Some studies have suggested that retaining a partner helps avoid survival costs (Ekman 1990, Pampus et al. 2005), while others have implicitly considered the influence of fidelity on survival by studying lifetime breeding success (Pyle et al. 2001). However, we are aware of only two studies (our own previous work on great tits, Culina et al. 2013: Chapter 3, and Nicolai et al.’s 2012 study on black brant geese) that have investigated the impact of fidelity on survival directly. Importantly, the majority of studies examining on the adaptive value of fidelity or divorce have compared the breeding success of pairs in different pairing outcomes, a process which by necessity ignores individuals whose breeding success is zero due to mortality. If individuals that change partners suffer survival costs (as we detected here for two species and three separate populations) then the conclusions of these studies as to whether pairing decision are adaptive or not are likely to be biased.

Our results revealed that the survival benefits of fidelity to a partner (or costs of partner change) were strikingly similar in two independent populations of great tits. Survival in great tits has been shown to depend on several extrinsic factors, such as environmental condition (e.g., temperature, winter snow cover), food availability, and interspecific competition (Clobert et al.

1988). While broad environmental conditions are likely to be shared by our two study populations, food availability and interspecific competition differ substantially, resulting in the variation in mortality rates. Accordingly, we observed population-specific annual variation in survival, but the same overall (i.e. long-term) survival rates in the two populations. It is not clear however, why this annual variation in survival did not translate into annual variation in the benefits of pair fidelity. In addition, we found no species-specific differences in the survival costs of fidelity between female great and blue tits, despite these two species surviving, on average, at different rates. However, we detected species-specific survival benefits of pair fidelity in males, these being higher for male great tits than for male blue tits. We suggest that these effects (i.e. difference in survival for males, but not for females) might be caused by differences in the social organisation of the two species (and sex-specific social position within flocks), and differences in the consequences of pairing outcomes for the breeding success of the two species and between sexes (Dhondt and Adriaensen 1994, Valcu and Kempenaers 2008, Culina et al. 2014: Chapter 2). Differentiating amongst these possible explanations requires further investigation.

Pair fidelity rates: overall level, fluctuation, and carry-over effects

The MECMR approach we used in our study allowed us to evaluate fidelity rates (and their correlates) in different species and populations under the same statistical framework while accounting for differences in recapture rates and for uncertainty in our ability to assign pair status. Our analyses revealed that the average long-term pair fidelity rates were similar in the two populations of great tits and in the blue and great tit populations, but showed different temporal patterns (in females) in the two great tit populations. This finding suggests that life-history traits and large-scale environmental conditions influence the overall level to which pair fidelity is expressed. In a recent comparative analysis, Botero and Rubenstein (2012) found that divorce rates across species correlate with the temperature predictability of the environment, with species forming short-term partnerships exhibiting lower divorce rates, and species forming long-term partnerships exhibiting higher divorce rates with the decrease in environmental predictability. However, reports on the population- and species-specific inter-annual variation in fidelity rates imply that local environmental effects that influence mortality rates are reflected in inter-annual changes in fidelity rates (Ens et al. 1993, Orell et al. 1994, Pyle et al. 2001, Maness and Anderson 2007). For example, Ens et al. (1993) have found that due to selective mortality of lower-quality breeders, there is an increase in divorce rates in oystercatcher (*Haematopus ostralegus*) population as more individuals of higher quality become available to pair with. Together with our results these reports indicate that studying species-specific pair fidelity rates in relation to large scale environmental factors, or species life history traits, should ideally be based upon assessments of fidelity rates over several years (or at least control for the length of the study period over which fidelity rates were taken).

Our MECMR analyses revealed that first year breeders have lower fidelity rates than do older individuals, a phenomenon reported in numerous studies (Ens et al. 1993; Choudhury 1995; Pampus et al. 2005; Llambias et al. 2008). Unlike other studies, however, the statistical approach we applied enabled us to demonstrate that the difference in pair fidelity between first year breeders and adults is shared between two different species and in two different populations of the same species. This suggests that age-specific pair fidelity might be determined by age-related intrinsic traits (i.e. individual quality, experience) rather than by environmental or demographic factors experienced by different populations. Interestingly, we did not find support that current pair status influences future pairing outcomes in any of the studied populations or species. We reported previously that fidelity rates in the Wytham Woods great tit population differed between birds that were already faithful, and those that were not (Culina et al. 2013: Chapter 3). The previous dataset encompassed a longer period of time (1979 to 2009) than that considered here (2001 to 2012). Hence, the inability to detect an effect in this study reveals the importance of long-term studies, even over several decades, to capture patterns of fidelity expressed in populations (Clutton-Brock and Sheldon 2010).

CONCLUSION

In conclusion, our study highlights the importance of considering survival when studying the fitness consequences of pairing outcomes, and suggests that survival costs of partner change and benefits of pair fidelity might be a widespread phenomenon in socially monogamous birds. Our results also reveal the necessity of accounting for differences in recapture rates among individuals when making inferences about correlates of pair fidelity. Furthermore, studies on the environmental and demographic correlates of fidelity that aim to explore among populations or among species patterns should be careful about the length of the time period over which the rates of population- or species-specific fidelity were obtained.

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SUPPLEMENTARY TABLES

Table S1. Summary results of the multi-event mark-recapture analysis to estimate recapture, survival, and pair fidelity rates in female great tits in Wytham Woods.

Parameter	recapture	survival	fidelity	np	dev	QAICc	Δ_i	w_i
recapture rates	state + t	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	47	15512.28	15607.36	0.00	0.83
	t			46	15517.44	15610.47	3.11	0.17
	constant			36	15577.97	15650.61	43.25	0.00
	state			37	15577.12	15651.79	44.43	0.00
survival rates	state + t	1y + AdN + AdR × state + t	1y + AdN + AdR x state + t	47	15512.28	15607.36	0.00	1.00
		1y + Ad × state + t		46	15543.83	15636.86	29.50	0.00
		1y + AdN + AdR + t		46	15577.99	15671.02	63.66	0.00
		1y + Ad + t		45	15587.44	15678.43	71.07	0.00
		t		44	15621.29	15710.23	102.87	0.00
fidelity rates	state + t	1y + AdN + AdR × state+t	1y + AdN + AdR + t	46	15512.28	15605.32	0.00	0.45
			1y + Ad + t	45	15515.44	15606.43	1.12	0.26
			1y + AdN + AdR × state + t	47	15512.28	15607.36	2.05	0.16
			1y + Ad × state + t	46	15514.93	15607.97	2.65	0.12
			t	44	15526.37	15615.31	10.00	0.00
			1y + Ad	35	15559.41	15630.01	24.70	0.00
			1y + AdN + AdR	36	15558.49	15631.12	25.81	0.00
			1y + Ad × state	36	15559.16	15631.80	26.48	0.00
			1y + AdN + AdR × state	37	15558.47	15633.14	27.82	0.00

Notation: state = pair status (pair faithful or partner changed); 1y = first year breeders; Ad = all adults , AdN = adults captured breeding for the first time while adults; AdR= adults already captured breeding (as adults or first year breeders) ; + = additive effect of covariates; × = interactive effect of covariates; np = number of estimable parameters; dev = deviance; QAICc = Akaike information criterion; Δ_i, the QAICc difference between the current model and the model with the lowest QAICc value; w_i = Akaike weight.

Table S2. Summary results of the multi-event mark-recapture analysis to estimate recapture, survival, and pair fidelity rates in male great tits in Wytham Woods. Notation is the same as in the Table S1.

Parameter	recapture	survival	fidelity	np	dev	QAICc	Δ_i	w_i
recapture rates	state + t	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	47	11582.97	11678.22	0.00	0.94
	t			46	11590.58	11683.77	5.56	0.06
	to			37	11616.53	11691.31	13.09	0.00
	constant			36	11626.07	11698.81	20.59	0.00
survival rates	state + t	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	47	11582.97	11678.22	0.00	1.00
		1y + AdN + AdR + t		46	11636.46	11729.65	51.44	0.00
		1y + Ad × state+t		46	11667.16	11760.36	82.14	0.00
		1y + Ad + t		45	11677.70	11768.85	90.63	0.00
		t		44	11681.30	11770.39	92.17	0.00
fidelity rates	state + t	1y + AdN + AdR × state + t	1y + AdN + AdR + t	46	11582.93	11676.13	0.00	0.74
			1y + AdN + AdR × state + t	47	11582.97	11678.22	2.09	0.26
			1y + Ad × state + t	46	11594.31	11687.50	11.37	0.00
			t	44	11601.07	11690.16	14.03	0.00
			1y + Ad + t	45	11599.42	11690.56	14.43	0.00
			1y + AdN + AdR	36	11618.16	11690.90	14.77	0.00
			1y + AdN + AdR × state	37	11618.15	11692.93	16.80	0.00
			1y + Ad × state	36	11632.11	11704.84	28.71	0.00
			1y + Ad	35	11636.37	11707.06	30.93	0.00

Table S3. Summary results of the multi-event mark-recapture analysis to estimate recapture, survival, and pair fidelity rates in female great tits in Bagley Wood. Notation is the same as in the Table S1.

Parameter	recapture	survival	fidelity	np	dev	QAICc	Δ_i	w_i
recapture rates	state	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	27	4193.18	4248.46	0.00	0.97
	state + t			32	4189.79	4255.59	7.13	0.03
	constant			26	4208.60	4261.79	13.33	0.00
	t			31	4203.91	4267.60	19.14	0.00
survival rates	state	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	27	4193.18	4248.46	0.00	0.97
		1y + Ad × state + t		26	4203.76	4256.95	8.49	0.01
		1y + AdN + AdR + t		26	4204.10	4257.29	8.83	0.01
		1y + Ad + t		25	4208.46	4259.56	11.10	0.00
		t		24	4246.47	4295.49	47.03	0.00
fidelity rates	state	1y + AdN + AdR × state+t	1y + Ad × state + t	26	4195.10	4248.29	0.00	0.33
			1y + AdN + AdR × state + t	27	4193.18	4248.46	0.17	0.30
			1y + AdN + AdR + t	26	4195.81	4249.00	0.71	0.23
			1y + AdN + AdR × state	22	4207.54	4252.39	4.10	0.04
			1y + Ad × state	21	4210.13	4252.91	4.62	0.03
			t	24	4204.23	4253.24	4.95	0.03
			1y + AdN + AdR	21	4211.61	4254.39	6.10	0.01
			1y + Ad + t	25	4203.99	4255.09	6.80	0.01
			1y + Ad	20	4221.56	4262.26	13.97	0.00

Table S4. Summary results of the multi-event mark-recapture analysis to estimate recapture, survival, and pair fidelity rates in male great tits in Bagley Wood. Notation is the same as in the Table S1.

Parameter	recapture	survival	fidelity	np	dev	QAICc	Δ_i	w_i
recapture rates	state	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	27	3455.60	3511.02	0.00	0.72
	constant			26	3461.01	3514.32	3.30	0.14
	t			31	3451.03	3514.90	3.88	0.10
	state + t			32	3450.73	3516.71	5.70	0.04
survival rates	state	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	27	3455.60	3511.02	0.00	0.95
		1y + AdN + AdR + t		25	3465.83	3517.05	6.03	0.05
		1y + Ad + t		24	3480.96	3530.08	19.06	0.00
		1y + Ad × state + t		25	3480.84	3532.06	21.04	0.00
		t		23	3490.86	3537.89	26.87	0.00
fidelity rates	state	1y + AdN + AdR × state + t	1y + Ad + t	25	3456.89	3508.11	0.00	0.35
			t	24	3459.62	3508.74	0.63	0.25
			1y + Ad × state + t	26	3456.50	3509.82	1.71	0.15
			1y + AdN + AdR + t	26	3456.56	3509.87	1.76	0.14
			1y + AdN + AdR × state + t	27	3455.60	3511.02	2.91	0.08
			1y+ Ad	20	3474.23	3515.02	6.90	0.01
			1y + Ad × state	21	3473.42	3516.28	8.17	0.00
			1y + AdN + AdR	21	3474.23	3517.09	8.98	0.00
			1y + AdN + AdR × state	22	3473.17	3518.11	10.00	0.00

Table S5. Summary results of the multi-event mark-recapture analysis to estimate recapture, survival, and pair fidelity rates in female blue tits in Wytham Woods. Notation is the same as in the Table S1.

parameter	recapture	survival	transition	np	dev	QAICc	Δ_i	w_i
recapture rates	state	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	37	13426.90	13501.63	0.00	0.66
	constant			36	13430.29	13502.98	1.35	0.34
	state + t			47	13418.63	13513.80	12.17	0.00
	t			46	13421.53	13514.65	13.03	0.00
survival rates	state	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	37	13426.90	13501.63	0.00	0.66
	constant	1y + AdN + AdR × state + t		36	13430.29	13502.98	1.35	0.34
	state	1y + Ad × state + t		36	13439.53	13512.22	10.60	0.00
	constant	1y + Ad × state + t		35	13443.39	13514.04	12.41	0.00
	state	1y + Ad + t		35	13452.28	13522.93	21.30	0.00
	constant	1y + Ad + t		34	13457.51	13526.13	24.50	0.00
	state	t		34	13468.92	13537.53	35.91	0.00
	constant	t		33	13477.65	13544.23	42.61	0.00
fidelity rates	state	1y + AdN + AdR × state + t	1y + Ad × state	26	13447.09	13499.45	0.00	0.15
	state		1y + AdN + AdR × state	27	13445.19	13499.58	0.13	0.14
	constant		1y + AdN + AdR × state	25	13449.69	13500.03	0.57	0.11
	state		1y + Ad × state + t	36	13427.82	13500.51	1.05	0.09
	constant		1y + Ad	24	13452.13	13500.44	0.99	0.09
	constant		1y + AdN + AdR × state	26	13448.33	13500.70	1.24	0.08

	state		1y + AdN + AdR × state + t	37	13426.90	13501.63	2.17	0.05
	constant		1y + Ad × state + t	35	13430.93	13501.58	2.13	0.05
	state		1y + Ad	25	13451.48	13501.82	2.36	0.05
	constant		t	33	13435.89	13502.48	3.02	0.03
	constant		1y + AdN + AdR × state	25	13452.10	13502.44	2.99	0.03
	constant		1y + AdN + AdR × state	36	13430.29	13502.98	3.53	0.03
	constant		1y + Ad + t	34	13434.78	13503.40	3.95	0.02
	state		t	34	13435.13	13503.74	4.29	0.02
	state		1y + Ad + t	35	13433.39	13504.04	4.59	0.02
	constant		1y + AdN + AdR	26	13451.47	13503.83	4.38	0.02
	constant		1y + AdN + AdR + t	35	13434.62	13505.28	5.82	0.01
	state		1y + AdN + AdR + t	36	13433.21	13505.90	6.45	0.01

Table S6. Summary results of the multi-event mark-recapture analysis to estimate recapture, survival, and pair fidelity rates in male blue tits in Wytham Woods. Notation is the same as in the Table S1.

Parameter	recapture	survival	transition	np	dev	QAICc	Δ_i	w_i
recapture rates	state	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	37	10094.63	10169.50	0.00	0.75
	constant			36	10099.45	10172.27	2.77	0.19
	state + t			47	10079.62	10175.03	5.52	0.05
	state			46	10083.93	10177.28	7.78	0.02
survival rates	state	1y + AdN + AdR × state + t	1y + AdN + AdR × state + t	37	10094.63	10169.50	0.00	0.68
	constant	1y + AdN + AdR × state + t		36	10099.45	10172.27	2.77	0.17
	state	1y + Ad × state + t		36	10100.71	10173.54	4.04	0.09
	constant	1y + Ad × state + t		35	10104.21	10174.99	5.49	0.04
	state	1y + Ad + t		35	10108.31	10179.10	9.59	0.01
	constant	1y + Ad + t		34	10110.85	10179.59	10.09	0.00
	state	t		34	10122.19	10190.93	21.43	0.00
	constant	t		33	10133.75	10200.44	30.94	0.00
fidelity rates	constant	1y + AdN + AdR × state + t	1y + Ad	24	10104.55	10152.92	0.00	0.24
	state		1y + AdN + AdR × state	27	10099.22	10153.69	0.77	0.16
	constant		1y + AdN + AdR	25	10103.45	10153.85	0.93	0.15
	state		1y + Ad	25	10103.77	10154.17	1.25	0.13
	state		1y + Ad × state	26	10102.44	10154.88	1.96	0.09
	constant		1y + Ad × state	25	10104.55	10154.95	2.03	0.09
	state		1y + AdN + AdR	26	10102.70	10155.13	2.21	0.08

	constant		1y + AdN + AdR × state	26	10103.12	10155.56	2.64	0.06
	state		1y + AdN + AdR × state + t	37	10094.63	10169.50	16.58	0.00
	constant		1y + Ad + t	34	10100.70	10169.44	16.52	0.00
	state		1y + Ad + t	35	10099.27	10170.05	17.13	0.00
	constant		1y + AdN + AdR + t	35	10099.68	10170.46	17.54	0.00
	state		1y + AdN + AdR + t	36	10098.01	10170.84	17.92	0.00
	state		1y + Ad × state + t	36	10098.02	10170.85	17.92	0.00
	constant		1y + Ad × state + t	35	10100.70	10171.48	18.56	0.00
	constant		1y + AdN + AdR x state + t	36	10099.45	10172.27	19.35	0.00
	state		t	34	10109.62	10178.36	25.44	0.00
	constant		t	33	10111.67	10178.37	25.44	0.00

Table S7. Summary results of the multi-event mark-recapture analysis to test for population specific (Wytham Woods and Bagley Wood) patterns of survival and pair fidelity rates in female great tits. Notation is the same as in the Table S1. Wyth = Wytham population; Bag = Bagley population; Pop = population (Wyth + Bag).

Parameter	Model structure for the tested parameter	Model structure for other parameters	np	dev	QAICc	w$_i$
Main model selection						
Recapture	state × Bag + t × Wyth	survival and fidelity both: [1y + AdN + AdR × state + t] × Pop	53	10746.32	10854.14	0.72
	state × Pop + t × Wyth		54	10746.15	10856.04	0.28
Survival	1y + AdN + AdR × state + t x Pop	recapture: state × Pop + t × Wyth fidelity:[1y + AdN + AdR × state + t] × Pop	51	10750.58	10854.27	0.60
	[1y + AdN + AdR × state + t] × Pop		54	10746.15	10856.04	0.25
	1y + AdN + AdR × state + t		46	10764.90	10858.27	0.08
	1y + AdN + AdR × state + t + Pop		47	10763.36	10858.79	0.06
	[1y + AdN + AdR × state] × Pop + t		50	10759.81	10861.43	0.02
	1y + AdN + AdR × state × Pop × t		56	10766.79	10880.82	0.00
Fidelity	1y + AdN + AdR × state + t × Pop	recapture: state × Pop + t × Wyth survival: 1y + AdN + AdR × state + t × Pop	48	10752.79	10850.28	0.88
	[1y + AdN + AdR × state + t] × Pop		51	10750.58	10854.27	0.12
	1y + AdN + AdR × state + t		43	10775.31	10862.51	0.00
	1y + AdN + AdR × state + t + Pop		44	10774.62	10863.87	0.00
	[1y + AdN + AdR × state] × Pop + t		47	10768.71	10864.14	0.00

Testing specific variation in parameters						
Survival	1y + AdN + AdR × state + Pop	recapture: state × Pop + t × Wyth fidelity: [1y + AdN + AdR × state + t] × Pop	43	10806.63	10893.83	0.57
	1y + AdN + AdR × state		42	10809.60	10894.74	0.36
	[1y + AdN + AdR × state] × Pop		46	10804.64	10898.02	0.07
	Ad × state × Pop		42	10832.34	10917.48	0.67
	Ad × state		40	10838.04	10919.08	0.30
Fidelity	1y + AdN + AdR ×state	recapture: state × Pop + t × Wyth survival: 1y + AdN + AdR × state + t × Pop	39	10788.95	10867.94	0.65
	1y + AdN + AdR × state + Pop		40	10788.31	10869.35	0.32
	[1y + AdN + AdR × state] × Pop		43	10786.49	10873.69	0.04
	Ad × state		37	10888.01	10962.90	0.88
	Ad × state × Pop		39	10887.92	10966.91	0.12
	t × Pop		45	10764.01	10855.32	0.99
	t		40	10784.37	10865.41	0.01
	t + Pop		41	10782.41	10865.50	0.01
	constant		36	10794.04	10866.88	0.62
	Pop		37	10792.96	10867.85	0.38

Table S8. Summary results of the multi-event mark-recapture analysis to test for population specific (Wytham Woods and Bagley Wood) patterns of survival and pair fidelity rates in male great tits. Notation is the same as in the Table S1. Wyth = Wytham population; Bag = Bagley population; Pop = population (Wyth + Bag).

Parameter	Model structure for the tested parameter	Model structure for the other parameters	np	dev	QAICc	w_i
Main model selection						
recapture	state + t + Pop	survival and fidelity both: [1y + AdN + AdR × state + t] × Pop	53	8296.07	8404.09	0.80
	state × Pop + t × Wyth		54	8298.06	8408.17	0.10
	state × Pop		50	8307.26	8409.07	0.07
	(state + t) × Wyth + Bag		53	8303.94	8411.97	0.02
	(state + t) × Pop		58	8294.19	8412.62	0.01
survival	[1y + AdN + AdR × state + t] × Pop	recapture: state + t + Pop fidelity: [1y + AdN + AdR × state + t] × Pop	53	8296.07	8404.09	0.48
	1y + AdN + AdR × state + t × Pop		50	8302.85	8404.66	0.36
	1y + AdN + AdR × state + t		45	8316.11	8407.57	0.08
	1y + AdN + AdR × state + t + Pop		46	8314.99	8408.52	0.05
	[1y + AdN + AdR × state] × Pop + t		49	8310.51	8410.24	0.02
	1y + AdN + AdR × state × Pop × t		56	8316.02	8430.29	0.00
fidelity	1y + AdN + AdR × state + t + Pop	recapture: state + t + Pop	46	8303.25	8396.78	0.45
	1y + AdN + AdR × state + t		45	8305.47	8396.93	0.42
	1y + AdN + AdR × state + t × Pop		50	8298.21	8400.02	0.09

	[1y + AdN + AdR × state] × Pop + t	survival: [1y + AdN + AdR × state + t] × Pop	49	8301.36	8401.09	0.05
	[1y + AdN + AdR × state + t] × Pop		53	8296.07	8404.09	0.01
Testing specific variation in parameters						
survival	1y + AdN + AdR × state	recapture: state + t + Pop fidelity: [1y + AdN + AdR × state + t] × Pop	41	8362.80	8446.01	0.43
	[1y + AdN + AdR × state] × Pop		45	8355.49	8446.95	0.27
	1y + AdN + AdR × state + Pop		42	8361.49	8446.77	0.30
	Ad × state		39	8391.53	8470.63	0.78
	Ad × state × Pop		41	8389.91	8473.12	0.22
fidelity	1y + AdN + AdR × state	recapture: state + t + Pop survival: [1y + AdN + AdR × state + t] × Pop	41	8325.43	8408.65	0.52
	1y + AdN + AdR × state + Pop		42	8323.77	8409.05	0.43
	[1y + AdN + AdR × state] × Pop		45	8321.97	8413.43	0.05
	Ad × state		39	8402.34	8481.48	0.85
	Ad × state × Pop		41	8401.70	8484.92	0.15
	t + Pop		43	8307.30	8394.63	0.77
	t		42	8312.77	8398.05	0.14
	Pop × t		47	8303.26	8398.85	0.09
	constant		38	8328.66	8405.71	0.56
	Pop		39	8327.14	8406.24	0.43

Table S9. Summary results of the multi-event mark-recapture analysis to test for the species specific (great and blue tits) patterns of survival and pair fidelity rates in females of Wytham Woods. Notation is the same as in the Table S1. GT = great tits; BT = blue tits; Sp = species (GT + BT).

Parameter	Model structure for the tested parameter	Model structure for other parameters	np	dev	QAICc	w_i
		Main model selection				
Recapture	State x Sp + t × GT	survival and fidelity both: [1y + AdN + AdR × state + t] × Sp	84	28939.18	29108.96	0.66
	(state + t) × GT + BT		83	28942.57	29110.31	0.34
Survival	1y + AdN + AdR × state + t × Sp	recapture: state × Sp + t × GT fidelity: [1y + AdN + AdR × state + t] × Sp	81	28941.15	29104.80	0.89
	[1y + AdN + AdR × state + t] × Sp		84	28939.18	29108.96	0.11
	1y + AdN + AdR × state + t + Sp		71	28989.65	29132.92	0.00
	[1y + AdN + AdR × state] × Sp + t		74	28988.20	29137.58	0.00
	1y + AdN + AdR × state + t		70	29009.23	29150.46	0.00
	1y + AdN + AdR × state × t × Sp		91	29019.16	29203.25	0.00
Fidelity	[1y + AdN + AdR × state] × Sp + t × GT	recapture: state × Sp + t × GT survival: 1y + AdN + AdR × state + t × Sp	71	28959.42	29102.69	0.50
	1y + AdN + AdR × state + t × GT		68	28967.25	29104.41	0.21
	[1y + AdN + AdR × state + t] × Sp		81	28941.15	29104.80	0.17
	1y + AdN + AdR × state + t × Sp		78	28948.09	29105.62	0.11
	1y + AdN + AdR × state + t		67	28991.41	29126.54	0.00
	1y + AdN + AdR × state + t + Sp		68	28990.12	29127.29	0.00
	[1y + AdN + AdR × state] × Sp + t		71	28984.48	29127.75	0.00

Testing variation in specific parameters						
Survival	1y + AdN + AdR × state + Sp	recapture: state × Sp + t × GT fidelity: [1y + AdN + AdR × state + t] × Sp	61	29039.63	29162.57	0.92
	[1y + AdN + AdR × state] × Sp		63	29038.28	29167.31	0.08
	1y + AdN + AdR × state		60	29060.20	29181.10	0.00
	Ad × state × Sp		60	29069.16	29190.07	0.52
	Ad × state		58	29073.37	29190.22	0.48
Fidelity	1y + AdN + AdR × state	recapture: state × Sp + t × GT fidelity: 1y + AdN + AdR × state + t × Sp	57	29013.86	29128.68	0.39
	1y + AdN + AdR × state + Sp		58	29012.14	29128.98	0.33
	[1y + AdN + AdR × state] × Sp		61	29006.36	29129.30	0.28
	Ad		54	29013.74	29130.59	1.00
	Ad × state × Sp		57	29190.31	29305.13	0.00
	Ad× state		55	29198.93	29309.69	0.00
	t × Sp		75	28964.41	29115.83	1.00
	t + Sp		65	29001.75	29132.82	0.00
	t		64	29007.78	29136.81	0.00
	Sp		55	29023.79	29134.56	0.53
	const		54	29026.10	29134.83	0.47

Table S10. Summary results of the multi-event mark-recapture analysis to test for the species specific (great and blue tits) patterns of survival and pair fidelity rates in males of Wytham Woods. Notation is the same as in the Table S1. GT = great tits; BT = blue tits; Sp = species (GT + BT).

Parameter	Model structure for the tested parameter	Model structure for other parameters	np	dev	QAICc	w_i
Main model selection						
Recapture	state × Sp + t × GT	survival: [1y + AdN + AdR × state + t] × Sp fidelity: [1y + AdN + AdR × state] × Sp + t × GT	74	21682.21	21831.83	0.72
	(state + t) × GT + BT		73	21686.11	21833.69	0.28
Survival	1y + AdN + AdR × state + t × Sp	recapture: state × Sp + t × GT fidelity: [1y + AdN + AdR × state] × Sp + t × GT	71	21687.94	21831.43	0.34
	[1y + AdN + AdR × state + t] × Sp		74	21682.21	21831.83	0.28
	1y + AdN + AdR × state + t + Sp		61	21722.12	21845.22	0.00
	[1y + AdN + AdR × state] × Sp + t		64	21716.68	21845.89	0.00
	1y + AdN + AdR × state + t		60	21734.61	21855.68	0.00
	1y + AdN + AdR × state × t × Sp		91	21717.90	21902.35	0.00
Fidelity	1y + AdN + AdR × state + t × GT	recapture: state × Sp + t × GT survival: [1y + AdN + AdR × state + t] × Sp	71	21685.75	21829.24	0.57
	1y + AdN + AdR × state × Sp + t × GT		73	21683.12	21830.70	0.27
	[1y + AdN + AdR × state] × Sp + t × GT		74	21682.21	21831.83	0.16
Testing variation in specific parameters						
Survival	[1y + AdN + AdR × state] × Sp	recapture: state × Sp + t × GT	54	21763.20	21872.06	0.58
	1y + AdN + AdR × state + Sp		51	21769.90	21872.67	0.42

	1y + AdN + AdR × state	fidelity: [1y + AdN + AdR × state] × Sp + t × GT	50	21784.49	21885.23	0.00
	Ad × state × Sp		50	21789.31	21890.05	0.98
	Ad × state		48	21801.54	21898.23	0.02
Fidelity	1y + AdN + AdR × state + Sp	recapture: state × Sp + t × GT survival: [1y + AdN + AdR × state + t] × Sp	61	21720.90	21844.00	0.47
	1y + AdN + AdR × state		60	21723.30	21844.37	0.40
	[1y + AdN + AdR × state] × Sp		64	21717.38	21846.59	0.13
	Ad		57	21894.93	22009.89	0.39
	Ad × state × Sp		60	21889.23	22010.30	0.32
	Ad × state		58	21893.55	22010.55	0.28
	t × GT + BT		68	21717.08	21854.44	1.00
	constant		57	21755.49	21870.46	0.00
	Sp		58	21754.89	21871.89	0.00

CHAPTER 5

Complex patterns of the influence of pair fidelity and partner change on future pairing outcomes, survival, and breeding in mute swans

Complex patterns of the influence of pair fidelity and partner change on future pairing outcomes, survival, and breeding in mute swans

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ABSTRACT

1. In socially monogamous birds, rates of pair bond maintenance between breeding seasons (i.e. pair fidelity rates) differ among species, population and individuals. To address what drives pair fidelity (including its breeding success consequences) studies either correlate these to population/species specific factors, or to a specific trait of interest (usually age), shared by a group of individuals.

2. However, these studies suffer from the variation in detectability of individuals and from the imperfect assignment of pair status. Consequently, conclusions about which external and internal factors influence fidelity may be biased. Moreover, exploring the potential survival or skipped breeding consequences of mating outcomes, as well as the influence of current pairing outcome on those in the future, becomes limited as information can only be obtained from those individuals that are captured, and which are likely to represent only a biased proportion of the population.

3. Here, we apply a coherent statistical framework (multi-event capture-mark-recapture approach) to simultaneously address drivers of individual differences in pair fidelity and in fidelity-fitness correlates in a mute swan *Cygnus olor* population over a 34 year period.

4. We show that breeding with the same partner decreases the likelihood of skipped breeding and increases survival to the next season. The effect is stronger in younger breeders (3-8 years

old) than in older swans, and in locally-born compared to immigrant females. We also show that fidelity (i) is higher for swans that have been faithful in the preceding season; (ii) depends on the stage of breeding lifetime (both sexes), and on breeding longevity (females); (iii) is higher for locally-born than immigrant males.

5. Our analyses demonstrate that multiple factors at the individual level influence pair fidelity and its fitness consequences. Such heterogeneity is likely to play an important role in the evolution of long-term partnerships.

INTRODUCTION

Long-lived annually breeding monogamous bird species generally show high pair fidelity rates from year to year (Bried et al. 2003). This is partly caused by low mortality rates (Bried et al. 2003, Jeschke and Kokko 2008), and the accumulation of reproductive benefits over repeated breeding with the same partner. Reproductive benefits might accrue both via a pair familiarity effect (Black 1996, Cezilly et al. 2000), and via the effect of breeding with experienced individual (Forslund and Part 1995). However, although often relatively high, pair fidelity rates are known to vary among species, among different populations of the same species (or over time within a population), and among individuals within populations. A common approach to understand these differences is to correlate fidelity rates to demographic and environmental factors at the species or population level (Ens et al. 1993, Dhondt et al. 1996, Marzluff et al. 1996, Maness and Anderson 2007). Another commonly applied approach is to group individuals within a population into different classes according to a shared trait of interest, and then to explore differences in fidelity rates between these classes. A frequently applied classification is according to age, where younger birds have repeatedly been found to have lower fidelity compared to older birds (Mougin et al. 2000, Pyle et al. 2001, Dreiss and Roulin 2014). This is usually attributed to poorer initial mate choice of younger birds, and to younger birds being more often left by their partners (or expelled by an intruder) than is the case with older, more experienced, birds (Ens et al. 1993; Choudhury 1995). Additionally, in a long-lived species with high rates of fidelity, finding a suitable partner early in life may be of great importance for lifetime fitness, and thus cause lower fidelity at the beginning of the breeding lifetime (Choudhury 1995).

However, studies of pair fidelity and its fitness consequences in wild populations are vulnerable to incorrect inference due to imperfect (i.e. less than 100%, e.g. Warkentin et al. 1991, Johnson and Walters 2008, Lachish et al. 2011) and potentially biased recapture rates (Pradel et al. 1997, Tavecchia et al. 2001, Crespin et al. 2008, Bouwhuis et al. 2012), especially if these biases arise due to pair status (i.e. breeding with the same or different partner compared to the last season, Culina et al. 2013: Chapter 3). To assign pair status to an individual with full certainty, the individual's previous and current partners have to be known (i.e. captured), a condition that is not always fulfilled. Consequently, several limitations to studying pair fidelity in wild populations may result. First, estimating fidelity rates could be based on a biased subset of individuals, and second, exploring differences in fidelity rates according to those individual traits that bias recapture can lead to inaccurate conclusions on the trait-specific rates of fidelity. Furthermore, potential survival costs are generally overlooked as possible fitness consequence of partner change in empirical studies, with only a few studies addressing this possibility (Nicolai et al. 2012, Culina et al. 2013: Chapter 3).

Apart from potentially flawed conclusions about the effects of individual traits on fidelity rates, the inability to assign individuals to a pair status if they (and/or their partners) are not observed prevents us from fully exploring if, and how, previous pairing outcomes influence future ones. In other contexts, modelling transitions between states has show that past states can influence the transition probability to future states. For example, Cory's shearwaters (*Clonectris diomedea*) that had skipped breeding or changed nesting site once are more likely to skip breeding or change the nesting site again (Sanz-Aguilar et al. 2011), and collared flycatchers (*Ficedula albicollis*) that had already dispersed are more likely to disperse again (Choquet et al. 2013). In a similar fashion, previous pairing outcomes might influence the probability of changing partner or staying faithful to the next season. Exploring the influence of the current pairing outcome on the future one can help us to elucidate selective pressures on pair fidelity that might be individual specific, and change through individual lifetime.

Given current gaps in the understanding of the factors influencing fidelity rates, and how these, in turn, might influence the evolution of long-term partnerships, we based our study around two main areas of interest. The first relates to the costs of partner change (or, alternatively, benefits of pair fidelity) for reproductive skipping and survival. The second relates to the factors that influence the probability of staying faithful or changing partner. We used data on pair composition from a long-term study of the mute swan (*Cygnus olor*), a long-lived bird previously suggested to have high fidelity and survival rates (Rees et al. 1996, Perrins and McCleery 1997, McCleery et al. 2002). Although mute swans have served as a paragon for monogamy and long-term partnerships in popular culture, not much is known about drivers of fidelity in the species (Black 1996). The three main factors that we considered to possibly influence survival and the rate of reproductive skipping were age, immigration status, and pair status. We considered the effects of four factors that can potentially influence the probability of staying faithful: stage of breeding lifetime, current pair status (i.e. breeding with the same or a different partner compared to the previous breeding season), individual quality (approximated by the individual breeding lifetime), and immigration status. All of these factors may potentially interact to produce different pressures on the costs and benefits of pair fidelity (or partner change) at different stages of individual lifetime. For example, birds at the beginning of their breeding lifetime might show lower fidelity rates as finding a compatible partner early in life is beneficial to lifetime breeding success (Choudhury 1995). Fidelity rates might also drop towards the end of the breeding lifetime, due to both increased mortality and divorce. Given that swans tend to pair assortatively by age (Perrins and McCleery 1997, Auld et al. 2013) older birds will more often lose their partners due to mortality. At the same time they might also get divorced more often as the reproductive value of breeders declines (McCleery et al. 2008, Auld et al. 2013).

To address the aims outlined above, we applied a flexible MECMR (Multi-Event Capture-Mark-Recapture) pair fidelity model that we have previously developed (Culina et al. 2013; Chapter 3) to 34 years of breeding data from colonial breeding mute swans. The framework is based around modelling of pair fidelity that uses principles of MECMR models (Pradel 2005, Pradel et al. 2008, Choquet et al. 2009) to accommodate biased and imperfect recapture rates, and uncertainty in the pair status assessment while studying the rates of interest (i.e. survival and fidelity). To differentiate which factors, and in what combination, influence rates of interest we compared the fit of the models with different constraints on the parameters of interest (see the Methods section).

METHODS

Abbotsbury swan population and data collection

Abbotsbury swannery (Dorset, 50°39’N, 2°36’W) was established more than 700 years ago. In contrast to other British, and most of the European populations, where pairs breed on isolated territories, mute swans at Abbotsbury breed colonially. The colony is not completely natural because adults and cygnets receive supplementary food. However, swans are free-ranging and pairing decisions are certainly unconstrained. A detailed description of the study site is provided in Perrins and Ogilvie (1981) and Perrins et al. (1994). Previously, rates of fidelity in this population have been assessed to be high, where 93% of males, and 88% of females, that survive between two breeding season stay with the same partner (Perrins and McCleery 1997); divorce rates have been reported to be very low (only 6% of pairs where both members survive, Perrins and McCleery 1997).

Data on pairings between individual swans at the colony have been collected since 1976. Birds are ringed as cygnets (majority of breeders, Perrins et al. 1994) or adults (10-20% of breeders in any given year are immigrants) with a standard BTO metal ring, and with an engraved plastic (darvic) ring. This allows for identification of swans even when not physically captured. During the breeding season nests in the main colony are identified and monitored by staff members on a daily basis. Monitoring includes identification of pair members, and detailed records on breeding parameters of pairs (see e.g. Perrins et al. 1994). Although the majority of breeders are recorded, early breeding failure (i.e. before hatching, Perrins et al. 1994), and nesting outside of the main colony may lead to some breeders being missed. The exact age for most of the birds is known, as they were ringed as cygnets at the colony; the exact age of immigrants can also be determined if they were captured in their first and/or second year. In this study we used data on observations (either sightings or physical captures) of breeding swans between 1979 and 2012. We included only birds of known age (96% of females and 93% of males originally present in the breeding dataset were of known age, and thus included in our analysis).

MECMR model of pair fidelity

To address the questions on drivers of the differences in pair fidelity rates and the fitness consequences of pair fidelity in a coherent statistical framework, we used an MECMR model of pair fidelity in birds (Culina et al. 2013: Chapter 3). In each breeding season, a bird can be in one three discrete states (Fig. 1): (i) breeding with the same partner as in the last season (faithful, denoted as ‘AS’); (ii) breeding with a different partner to the last season (partner changed, denoted as ‘AD’), and (iii) dead (denoted as ‘D’). Movement between the states happens between two successive breeding seasons, and is composed of two steps: survival (‘Φ’ denotes survival probability) followed by fidelity (‘Ψ’ denotes probability to stay faithful, conditional on survival). The ‘dead’ state is an absorbing state (i.e. once dead, a bird cannot move to any other state). A bird that is in an alive state (either faithful or partner changed, we call this pair status) in the breeding season *t* first survives (or dies), and then, conditional on its survival, either stays in the current pair status, or transitions to the other one in the season *t+1*. The transition probabilities (i.e. survival and fidelity) are represented in two matrices: the survival matrix and the pair fidelity matrix (see Culina et al. 2013, Appendix to Chapter 3, Section 1).

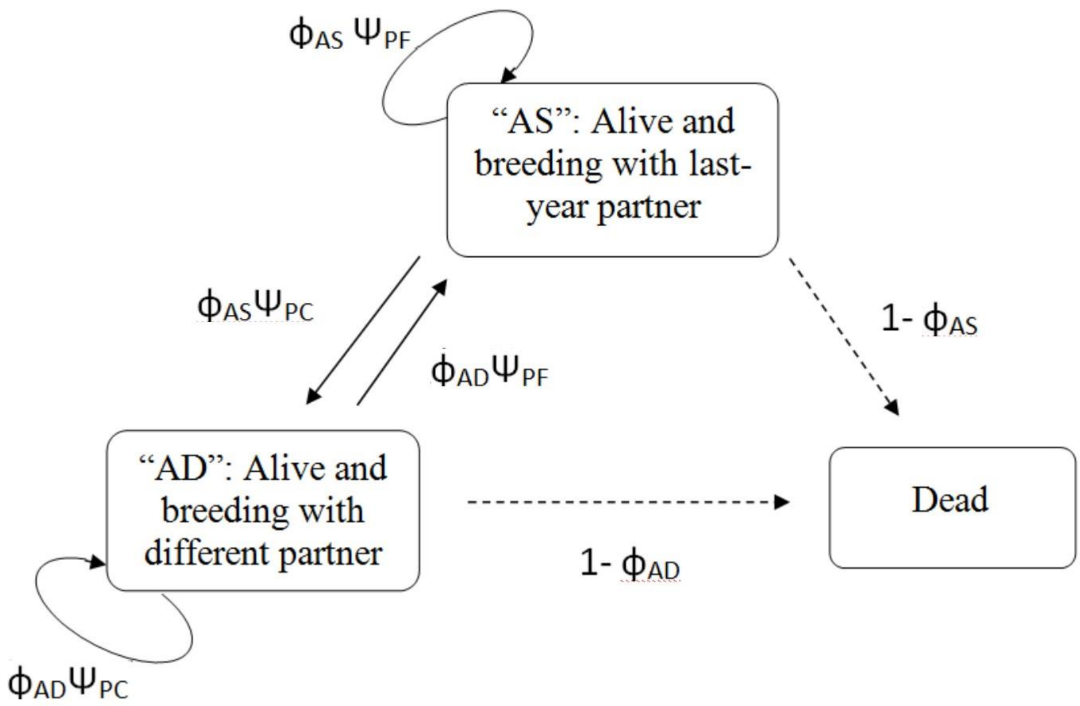

Figure 1. Illustrative figure of the transitions between states used to estimate rates of pair fidelity and partner change in mute swans. Φ = survival probability: ϕ_{AS} = survival probability for individuals breeding with their previous partner (i.e. pair faithful individuals); ϕ_{AD} = survival probability for individuals that have changed partner. Ψ = transition probability conditional on survival: Ψ_{PC} = probability of changing partner; Ψ_{PF} = probability of staying with the same partner (i.e. pair fidelity rate).

Although we are ultimately interested in states (and transitions among them), observations of individuals do not always allow for a state to be assigned with absolute certainty, because this requires that the focal bird was observed in subsequent breeding seasons, and that its partners in both seasons were known. Consequently, to infer the underlying state we use series of conditional probabilities relating the real state that individual is in at each breeding season to our observations (termed ‘events’). These conditional probabilities are composed of the recapture (i.e. either resighting, or physical capture) probability of the focal bird (conditional on it being alive and breeding), probability of capturing its current (*t*) partner and knowing its relation to the *t*-1 partner (same or different), and recapture probability of the *t*-1 partner in the current (*t*) breeding season, combined with the knowledge on its current (i.e. in *t*) pairing status. The event probabilities are represented in three event matrices, respectively: focal bird recapture matrix, current partner capture matrix, and previous partner capture matrix (see Culina et al. 2013, and Appendix to Chapter 3, Section 1). Given the observation process, in the study population (as in most similar such populations) there are seven possible (discrete) events (coded between ’0’ and ’6’). Some of these events correspond to only one state (i.e. events 1, 2, and 4), and some to more than one state (the remaining events):

- event 0 = the focal bird was not observed in the current breeding season (at *t*), its partner from the previous season (*t*-1) was either not observed at *t*-1 or *t*, or was observed breeding at *t* at an active nest with an unknown partner. This event can correspond to all three possible states;
- event 1 = the focal bird was observed at *t*, and was breeding with its partner from *t*-1. This event corresponds to ‘AS’ state (alive and breeding with the same partner).
- event 2 = the focal bird was observed at *t* and was breeding with a different partner to that from *t*-1. This event corresponds to ‘AD’ state (alive and breeding with a different partner);
- event 3 = the focal bird was observed at *t* but it was not known whether its current partner, which was observed, was the same as the one from *t*-1. This event can correspond to ‘AS’ or ‘AD’ state;

- event 4 = the focal bird was observed at *t*, its current partner was not observed, but its partner from *t*-1 was observed at *t* at a different nest (and hence was not breeding with the focal bird at *t*). This event corresponds to 'AD' state;
- event 5 = the focal bird was observed at *t*, its current partner was not observed, and its partner from *t*-1 was either not observed in *t* or was not known in *t*-1. This event can correspond to 'AS' or 'AD' state;
- event 6 = the focal bird was not observed at *t* (and hence its current partner was unknown), but its partner from *t*-1 was captured breeding with another individual at *t*. This event can correspond to 'AD' or 'Dead' state.

Application of the MECMR model to fidelity in mute swans

We ran the MECMR models in E-SURGE Version 1.8.5 (Choquet al. 2009b; Choquet and Nogue 2011), and provide further details about implementation in the Appendix to Chapter 3 (Sections 2 and 4). We tested different hypotheses about what influences parameter values by constraining the parameters of interest, and comparing the performance of models with different structures in terms of the AIC values (Burnham and Anderson 2002). If the AIC difference of the two models was 3 or greater, we considered the model with the lower AIC value to be the better supported one.

To model the recapture rates (reflecting skipped breeding) we considered the influence of age since first capture (between 1st and 5th breeding season, and older), the pair status the focal individual was in (i.e. breeding with the same partner as in the last season, or breeding with a different partner to the last season), and time (i.e. year of study). We based the age categorisation on the previous findings on the recapture rates in the colony, where the recapture rate was found to slightly increase by the age of five, and then to remain constant (McCleery et al. 2002). Because (i) of the way our modelling framework was defined (i.e. recapture rates are recapture rates conditional on birds being alive and present at the colony); (ii) we know that emigration after first breeding is low in the studied population (Charmantier et al. 2006a, McCleery et al. 2008, Auld et al. 2013); and (iii) a very thorough monitoring protocol ensures that majority of breeders is detected, low recapture rates should reflect skipped breeding. We note here that a more suitable term to use when allocating a bird to a pair status would be ‘birds that have not stayed with their partners’. This term, compared to ‘birds that have changed partners’ does not imply that a bird must find a new partner after the partnership with the old one has been terminated, but allows for the possibility of skipped breeding instead.

To model survival we considered chronological age, current pair status, and time (i.e. year) as possible influential factors. We used two age classes to model survival: birds between 2 and 8 years old (no bird started breeding at age 1), and older, based on the previous studies modelling survival in the same colony (McCleery et al. 2002, McCleery et al. 2008, Wood et al. 2013). To model fidelity we considered age since the first capture, current pair status, and time (i.e. year) as possible influential factors. We split the age since the first capture into either two levels (between 1st and 2nd breeding season, and after 2nd breeding season) or three levels (between 1st and 2nd, between 2nd and 8th, and after 8th breeding season). We did this with the main aim to test if fidelity rates are lower after the first breeding season, and at older ages. In addition, we allowed that fidelity between first and second breeding season depended on the age of the first breeding (2-8 years old, or 9 and older) to accommodate the possibility that birds that start to breed at late ages face different constraints on future breeding compared to birds that start breeding at earlier ages.

For each sex we created separate capture histories (representing the series of events observed for different years) using the data from 1979 - 2012 (740 individual females and 806 males; 3588 breeding attempts). Because the models were computationally demanding (e.g. taking 3 days on Dell, 8.00GB RAM, Core(TM) i7 CPU at 2.80 GHz computer), we used some of the conclusions from model selection on the female data (which we ran first) to decrease the complexity of the models tested in the male dataset (e.g. selection on the females dataset revealed time-dependence in fidelity rates, so we only considered time-dependence in fidelity in male dataset). However, we were cautious not to exclude any biologically plausible differences between males and females. The full list of models is given in Supplementary Tables S3&4. We first modelled recapture rates, while keeping survival and fidelity rates fully parameterised. Next, we modelled survival rates, constraining the recapture part of the model as selected in the previous step, and keeping fidelity rates fully parameterised. Finally, we modelled fidelity rates while keeping recapture and survival as selected in the first two steps.

To further explore whether there are any differences in fidelity rate related to the quality of breeders, we used breeding longevity (i.e. number of breeding seasons elapsed between the first and the last year of breeding) as a proxy for quality. We considered that breeding longevity should be a good proxy for individual quality based on the results of the previous studies on the same population (Charmantier et al. 2006b, McCleery et al. 2008, Auld et al. 2013). Charmantier et al.'s (2006) study suggested that individuals vary in their inherent quality, with some individuals having earlier age of first reproduction, and later age of last reproduction than expected. We defined six different breeding longevity classes: 1 year, 2 years, 3-4 years, 5-6 years, 7-10 years, 11 years or longer. Given that the lowest breeding longevity for the final quality category was 11 years, we 'trimmed' the original capture histories up to (and including) year 2001. This procedure ensured that no bird whose breeding longevity was more than 11 years ended up being classified as having breeding longevity less than 11 years (due to data being censored). The 'trimmed' dataset consisted of recapture histories of 476 females and 509 males. To reduce computation time, we used the results of the previous model selection (i.e. on the full dataset) to decide on the parameter variation regarding the effects of time, pair status and age. However, in addition (and given we were primarily interested in fidelity rates) we also reduced the complexity of the survival part of the model structure (which was, because of the way age has to be defined in these models, computationally demanding) so that it included only age since the first capture, but not the chronological age. For the same reason, we excluded the age from the recapture part of the models run on the female dataset (in males there was no support for age-dependent recapture in the original dataset). The list of all models tested is given in Supplementary Table S5.

To explore how immigration status influenced fidelity rates, and the survival and skipped breeding (reflected in the recapture rates) consequences of fidelity we used the 'trimmed' dataset. We explored different combinations of possible additive and interactive effects of immigration status on recapture rates, survival rates, and pair fidelity rates (Supplementary Tables 6&7), and compared the performance of models with different structures.

Goodness-of-fit test

Before we ran the model selection, we performed the goodness-of-fit (GOF) on the single-state data as it is not currently possible to perform the GOF test for MECMR models. We did this using raw captured/non-captured histories (i.e. coded ‘1’ = captured; ‘0’ = non-captured). Here the codes ‘1’ and ‘0’ replaced any multi-event code from the original capture histories corresponding to focal being or not being observed at the capture occasion, respectively. We assessed the fit of three possible starting general models to our data: (i) the Cormack-Jolly-Seber (CJS) model with time-dependent survival and recapture (see Lebreton et al. 1992); and (ii) the immediate ‘trap-dependence’ version of the CJS model (see Pradel 1993) where recapture rates at $t + 1$ are different between individuals captured and not captured at the capture occasion t. We did this as we expected that there might be a heterogeneity in recapture rates amongst individuals due to skipped breeding. In this case the ‘trap-dependence’ model, rather than the simple CJS model would be the appropriate general model, as it would account for overdispersion caused by capture heterogeneity. We preformed the GOF test in the program U-CARE (Choquet 2005). The most relevant statistics for the detection of trap-dependence provided in U-CARE is one-sided directional (z) statistic from the Test2.CT (Pradel et al. 2005). We used the approach described by Peron et al. 2010 to approximate a GOF test for time-depended model with capture heterogeneity and to account for possible sources of trap-dependence, if any. We did this by (i) computing the overall statistics for trap-dependence (i.e. from U-CARE Test2); (ii) computing the directional statistics from the Test2.CT; (iii) removing the squared directional statistics from the overall statistics. If, after accounting for trap-dependence, the overdispersion coefficient (calculated as χ^2/d.f.) was still large (i.e. >2), overdispersion parameter needed to be accounted for in the model selection (however, this was not the case with our data, see Results).

Calculation of divorce rates

Our modelling framework does not distinguish between divorce (pairs where both members survive between the two seasons, but do not breed together) and widowing (only one member of a pair survives). However, it is possible to calculate the divorce rates in each sex by using fidelity rates of one sex (e.g. females), and mortality rates of the opposite sex (e.g. males), using the following formula:

$$\text{divorce} = (1\text{-fidelity}_{\text{females}}) \times \text{survival}_{\text{males}} / \,[(1\text{-fidelity}_{\text{femles}}) \times \text{survival}_{\text{males}} + \text{fidelity}_{\text{females}}] \qquad \textbf{[1]}$$

where $(1\text{-fidelity}_{\text{females}}) \times \text{survival}_{\text{males}}$ calculates the divorce rates of females amongst all of the surviving females (i.e. divorce/(divorce+widowing+fidelity)), and the overall formula translates this into divorce rates amongst females whose partners stayed alive (i.e. divorce/(divorce+fidelity)).

Depending on the structure of the best model selected for each sex, it is possible to calculate either exact or approximate divorce rates. For example, divorce rates to the next breeding season (i.e. between t and $t + 1$) of females that were previously faithful to their partner (i.e. have stayed with the same partner between $t - 1$ and t) can be calculated from the fidelity rates between t and $t + 1$ of faithful females and the survival rates (between t and $t + 1$) of faithful males (faithful females must be paired with faithful males). On the other hand, the divorce rates of females that have changed partner can only be approximated (partner changed females can be paired either with partner changed males, or with new breeders). However, given that swans in the population pair assortatively by age (Perrins and McCleery 1997, Auld et al. 2013), it is most likely that females that changed partners bred with other males that changed partners, rather than young breeders.

RESULTS

The earliest age swans in the studied colony started to breed was at 2 years, and the latest at 18 years. The majority of birds (80% of females, and 77% of males) started to breed between 3 and 5 years of age. In the overall dataset, 14% of females and 26% of males were immigrants. Breeding longevity varied between 1 and 20 years in females (mean = 6.08, sd = 4.65; median = 5), and between 1 and 17 years in males (mean = 5.22, sd = 3.79; median = 4).

Goodness-of-fit

As expected, GOF tests detected heterogeneity in recapture rates, with significant trap-happiness detected for both females and males (i.e. the directional test for trap-dependence was statistically significant and negative, see Supplementary Tables S1&2). The other components of the GOF were not significant in any dataset. After correcting for the trap-happiness, the overdispersion coefficients were not larger than the critical value of 2 (Supplementary Tables S1&2). These results indicated that a time-dependent model with heterogeneity in recapture rates fitted the data. After their initial capture and marking, breeders in our study population are never again physically captured, but are rather sighted from a distance. Hence, in this instance the trap-happiness we detected is unlikely to be a consequence of behavioral trap-happiness and rather reflects differences in the sighting probability for long-term partners and new partners. We thus accounted for the heterogeneity in recapture rates by modeling recapture rates as a function for pair status (i.e. breeding with the same, or a different partner to the last breeding season).

Previous pairing outcomes and age influence pair fidelity rates and costs of partner change

Model selection revealed that in female swans (i) recapture rates varied with time and depended on age since first capture (between 1st and 5th breeding season, or later) and the pair status a female is in; (ii) survival rates varied with time and depend on the chronological age and pair status; and (iii) fidelity rates varied in time and depended on age since first capture (between 1st and 2nd breeding season, or later) and pair status (Supplementary Table S3). While females breeding with the same male as in the previous breeding season had recapture rates very close to 1 (and consequently time variation was not detected), recapture rates of females that had not stayed with the same partner were much lower (Fig 2A), ranging between 0.04 (95% CI = 0.01-0.14) and 0.77 (95% CI = 0.40-0.94). This finding indicates that females that have not kept the partner from the previous season suffer a substantial cost of skipped breeding (and thus show lower recapture rates), and that this cost is different in different years. The likelihood of skipped breeding was slightly higher for females at the beginning of their reproductive lifetime (i.e. between their 1st and 5th breeding season) than later (Fig 2A). However, the result must be interpreted with caution because the effect could also be due to selective disappearance of lower quality individuals.

In addition to skipped breeding, females that changed partners also suffered lower survival to the next breeding season compared to the faithful females (Fig 3A). The difference in survival between faithful birds and birds that changed partner was greater for 2 to 8 year-old birds (faithful: 0.95, 95% CI = 0.92-0.96; changed: 0.68, 95% CI = 0.62-0.73) than for birds older than 8 years (faithful: 0.85, 95% CI = 0.82-0.88; changed: 0.71, 95% CI = 0.66-0.76), indicating that females of different ages apparently experience different benefits of pair fidelity.

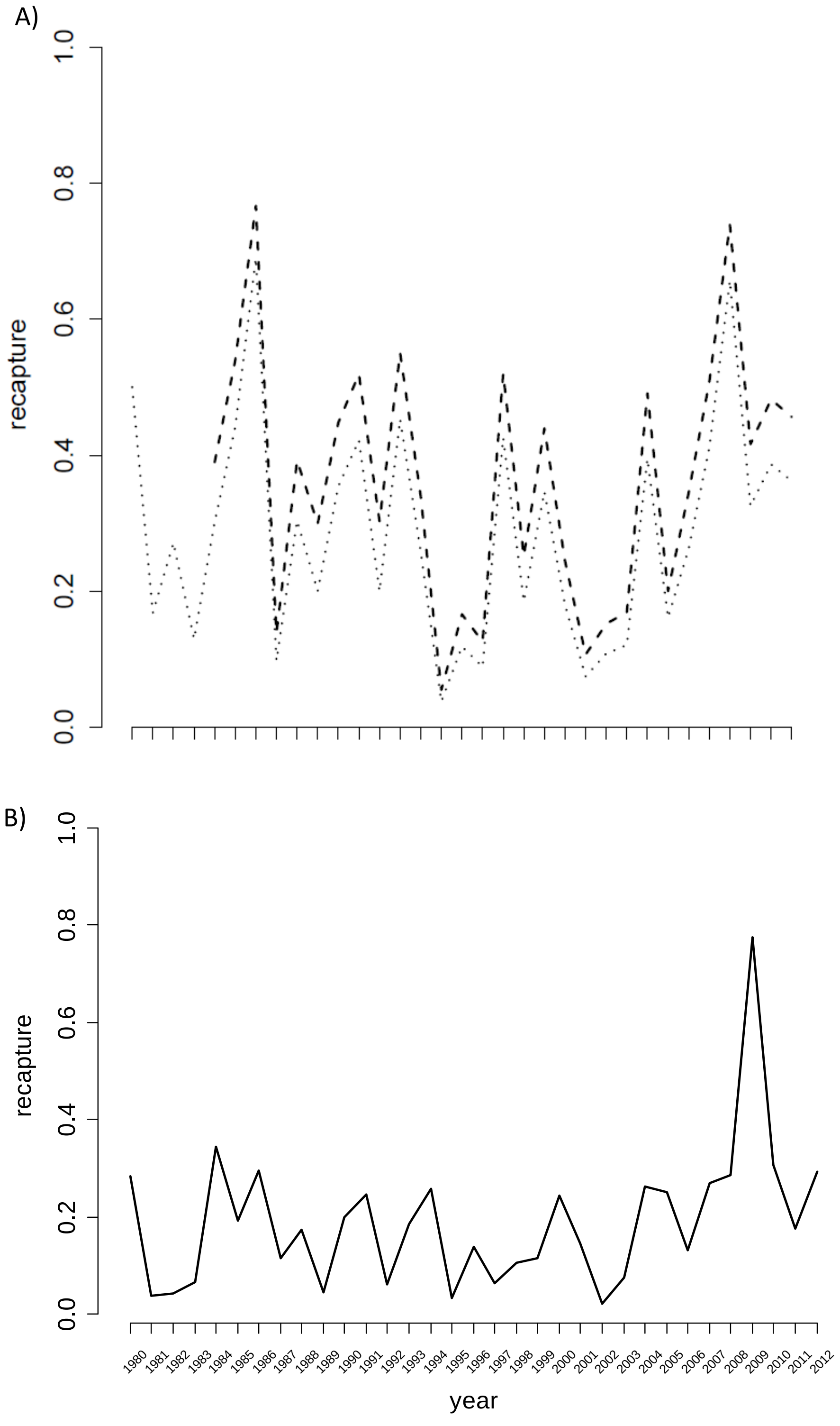

Figure 2. Estimates of the recapture rates of breeding (A) female and (B) male mute swans that bred with a different partner compared to the previous breeding season between 1979 and 2012. Estimates are as obtained by the best model in each sex. For females these are given for females breeding between their 1st and 5th breeding season = dotted line and between 5th and later breeding seasons = dashed line.

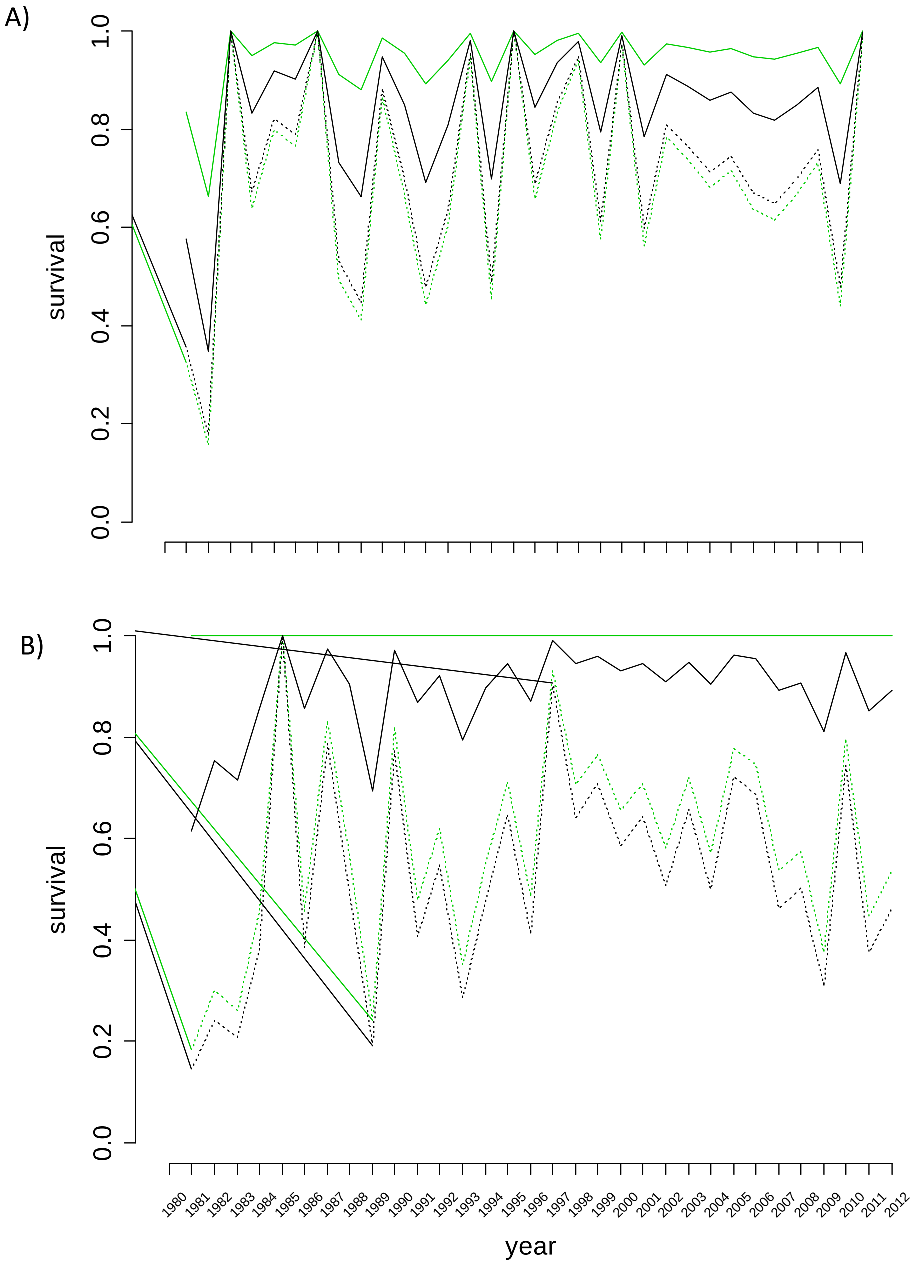

Figure 3. Estimates of the survival rates of breeding (A) female and (B) male mute swans according to their pairing status (faithful = full lines, partner changed = dotted lines) and age (2 to 8 years old = green, 9 years or older = black) between 1979 and 2012. Estimates are as obtained by the best model in each sex.

Finally, previously faithful females showed higher fidelity rates compared to females that had already changed their partners (Fig 4A). In other words, previous pairing outcomes influenced future pairing outcomes. Fidelity rates of females between their 1st and 2nd breeding season were slightly lower (0.74, 95% CI = 0.69-0.78) than fidelity rates of faithful females (i.e. those females that have bred at least once, 0.76, 95% CI = 0.74-0.79), but higher than fidelity rates of females that had already changed partner (0.40, 95% CI = 0.36-0.45). By calculating the divorce rates for females (using the survival in the corresponding group of males) we found that the difference in fidelity rates between the two pairing classes was largely due to previously faithful females having lower divorce rates compared to females that had changed partners; already faithful females were only half as likely to divorce to the next season. Divorce rates of partner-changed females were on average 0.44 (sd = 0.16) and of faithful females 0.25 (sd = 0.13) over the study period. We did not find support for a drop in fidelity rates at older ages.

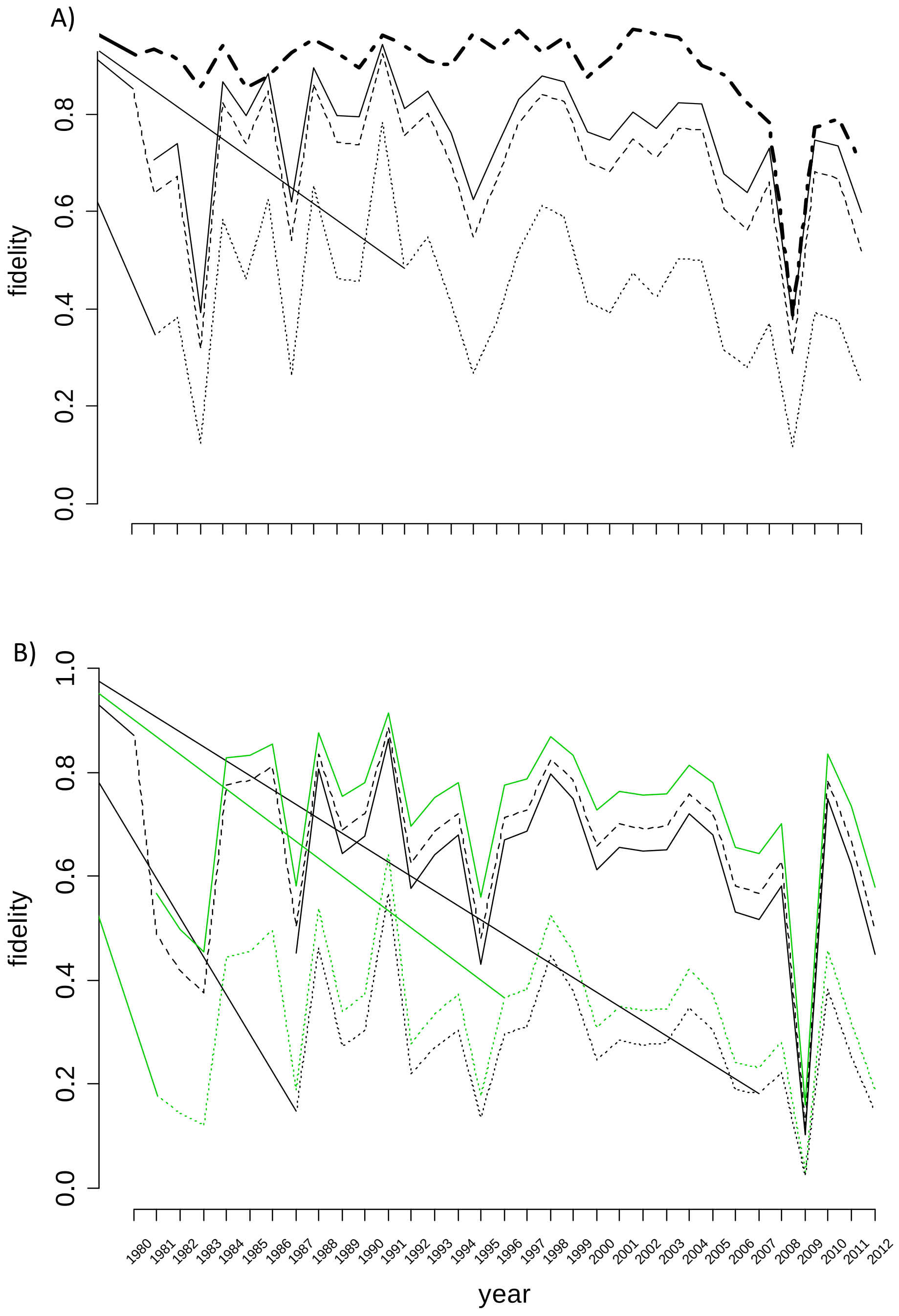

Figure 4. Estimates of the pair fidelity rates of breeding (A) female and (B) male mute swans according to their pair status and stage in the breeding lifetime between 1979 and 2012. Fidelity rates between 1st and 2nd breeding season are given as the dashed line, and as full (faithful) or dotted (partner changed) line for adult breeders (i.e. after their second breeding season). In addition, for males fidelity rates are plotted separately for males breeding between their 2nd and 8th breeding season (green lines) and after 8th breeding season (black). Estimates are as obtained by the best model in each sex. Pair fidelity rates obtained by traditional methods, are given in the graph for females.

We found broadly similar patterns of time and pair status-dependence in recapture (i.e. reflecting skipped breeding if low) and survival rates in males as we found in females, except that recapture rates did not depend on age (summary of the model selection is given in the Supplementary Table S4). Recapture rates for males breeding with the same partner as in the last season were 1, while they ranged between 0.02 (95% CI = 0.01-0.10) and 0.77 (95% CI = 0.63-0.87) for males that did not keep their former partners. This implies that in some years almost all of the males that did not keep their partners skipped breeding in the next breeding season. Survival benefits of pair fidelity were age-dependent (Fig 3B). Males between three and eight years of age survived at 0.99 (95% CI = 0.98-1) if faithful to the partner, and at 0.58 (95% CI = 0.50-0.60) if not. Older birds survived at 0.89 (95% CI = 0.88-0.91) if faithful, and at 0.52 (95% CI = 0.40-0.61) if they changed a partner. In contrast to the female dataset, we found support for fidelity rates dropping at the later stages of breeding lifetime. Fidelity rates were highest for males between their 2nd and 8th breeding seasons, lower for males between the 1st and 2nd breeding season, and lowest of all after the 8th breeding seasons (Fig 4B). Fidelity was also higher for already faithful males of any stage of breeding lifetime (2nd to 8th breeding season: 0.72, 95% CI = 0.60-0.78; after 8th season: 0.62, 95% CI = 0.54-0.70) than for males that had already changed partners (2nd to 8th breeding season: 0.34, 95% CI = 0.27-0.40; after 8th season: 0.28, 95% CI = 0.11-0.33). As with females, this was largely due to two-fold higher divorce rates of males that had already changed partners (2nd to 8th breeding season: 0.57, sd = 0.15; after 8th season: 0.65, sd=0.13) compared to males that had already been faithful (2nd to 8th breeding season: 0.27, sd=0.15; after 8th season: 0.34, sd = 0.15).

Pair fidelity, divorce and individual quality

Model selection on the female dataset gave a strong support to the models in which quality (which we assumed to be related to the breeding lifespan) influenced fidelity rates (Supplementary Table S5). The patterns of estimated fidelity rates shown by females in different quality classes and at different stages in the breeding lifetime were complex (see Fig 5). Similarly, when we calculated divorce rates, using the formula [1], it was evident that the contribution of divorce to the overall partner change (i.e. both divorce and windowing) was quality and stage specific. The results of the best model supported our hypothesis that females with longer lifespan (i.e. longer than 6 years) show a reduction in fidelity rates at the end of their breeding lifetime, and this seems to be mainly caused by divorce. On the other hand, the results of the best model were not consistent with our prediction that birds with longer lifespan show higher divorce rates at the beginning of their breeding lifetime, compared to shorter lived birds. Model selection on the male dataset did not give support to the models where quality influenced the probability of a male to stay faithful (Supplementary Table S5).

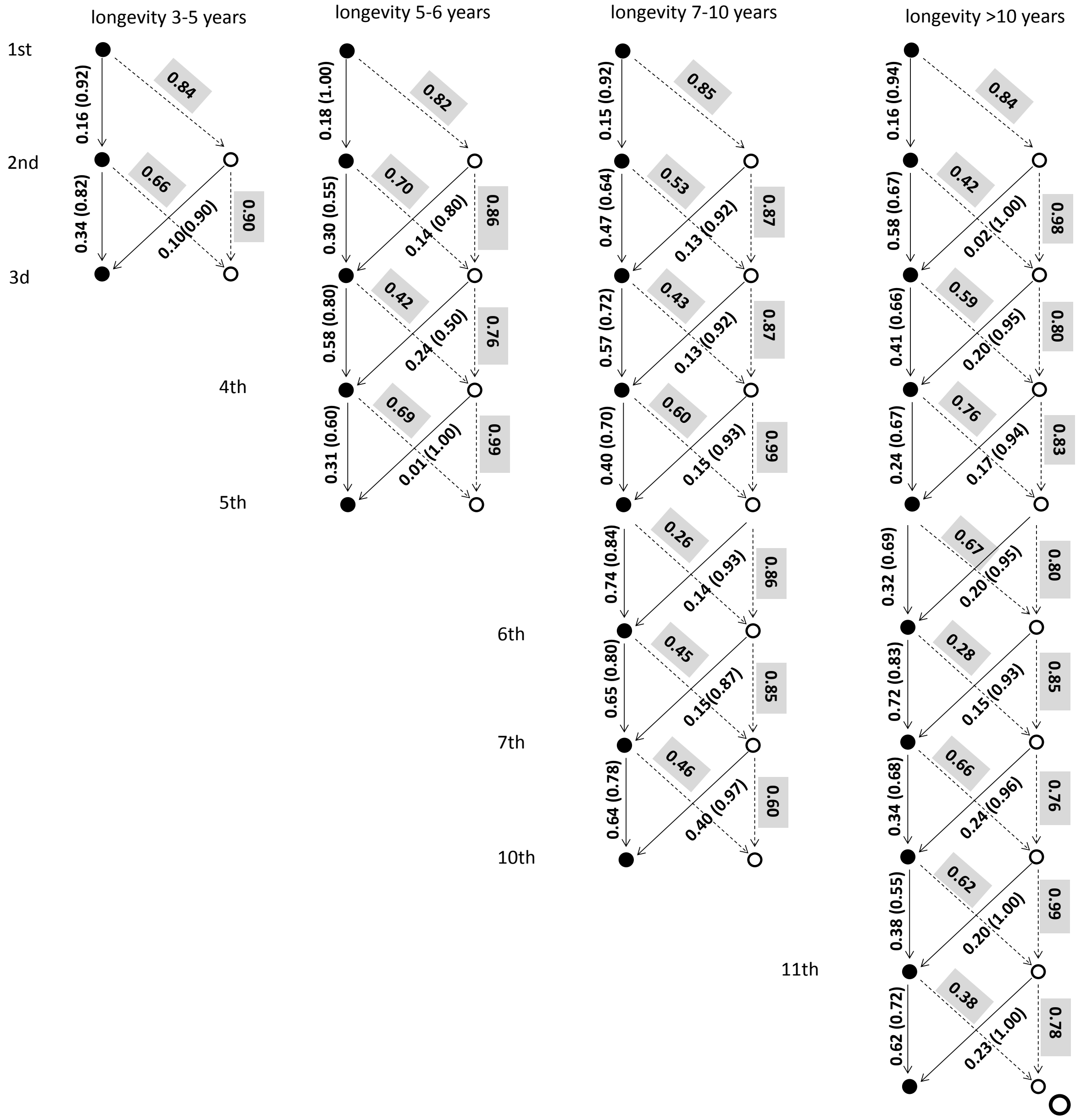

Figure 5. Probability of pair fidelity and partner change (due to widowing or divorce) through time for female mute swans differing in reproductive lifespan (3-5 years, 5-6 years, 7-10 years, longer that 10 years) according to female pair status (pair faithful = open circles, or partner changed = filled circles) and stage in the breeding lifetime. Full lines represent the probability to change partner between the two seasons, and dashed lines the probability to stay with the same partner between the two seasons. Corresponding rates are given above each line. Because partner change can happen due to divorce or widowing, the probability that divorce is the cause of partner change is given in the brackets. For example between the 2nd and 3^{d} breeding season, a female swan that has already changed a partner (black circle) has probability 0.70 to stay with that partner and 0.30 to change it. If it changes partner, the probability that the change is due to divorce is 0.55.

Immigration status

Model selection on the influence of immigration status on fidelity rates and costs of partner change in female swans resulted in four models gaining similar support (i.e. delta AIC<1, Supplementary Table S6). However, there was a clear support for models where the magnitude of the difference in survival between faithful and partner-changed females was dependent on the immigration status. The difference in survival between faithful and partner-changed females was larger for resident than for immigrant females (where there was almost no difference in survival, Fig 6), and decreased with the stage of breeding lifetime. The survival of resident females that stayed with the same partner between their first and second season was almost twice as high as the survival rate of females that changed their partner, while there was no difference in the survival of birds of different pairing status after the 8th breeding season. These results indicate that resident females might benefit from pair fidelity more than immigrant females, especially earlier in their breeding lifetimes. Model selection on the female dataset yielded no support for the existence of the difference in skipped breeding and fidelity rates between immigrant and resident females. Models with immigration status (interactive with 'pair status') and without the immigration status in the recapture part of the model gained similar support, as well as did models with (as additive effect) and without the immigration status in the fidelity part of the model.

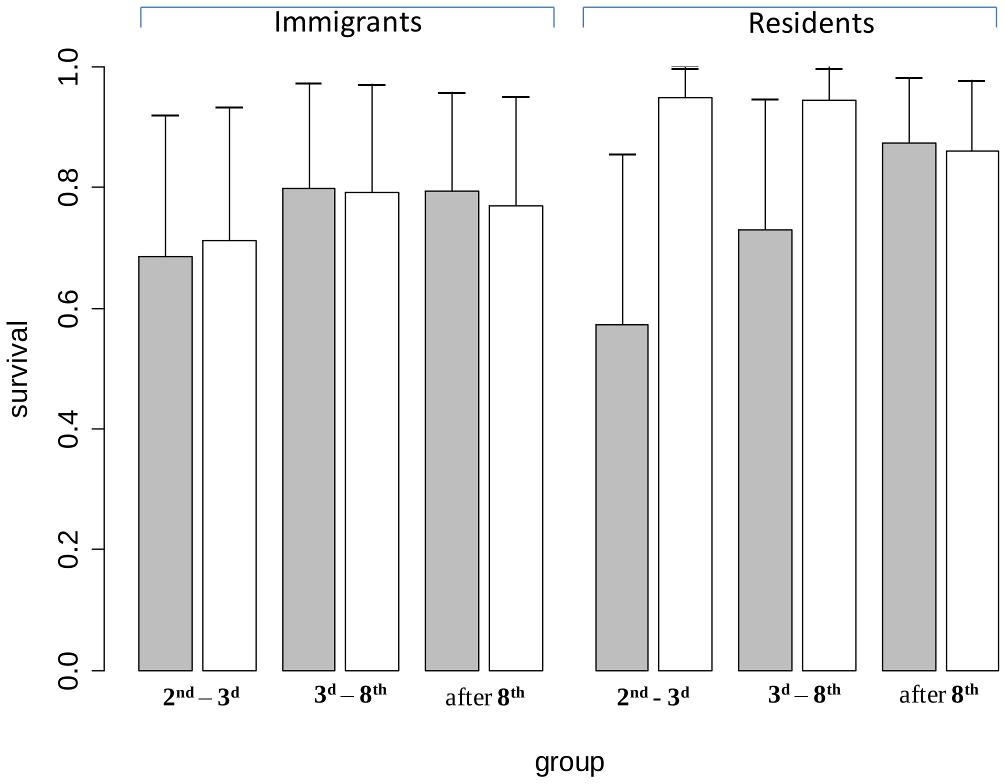

Figure 6. Costs of partner change in terms of reduced survival in female immigrant and resident mute swans (with 95% CI of the estimate). Gray bars = birds that have changed partners, white bars = faithful birds. Survival rates are estimated for birds between their 2nd and 3d breeding season, between 3d and 8th breeding season, and after 8th breeding season.

Model selection on the male dataset (Supplementary Table S7) yielded strongest support for the model where survival, and fidelity rates, but not recapture rates (i.e. reflecting skipped breeding), were different between immigrant and resident males. Immigrant males had lower survival rates, but the survival costs of partner change (i.e. the difference in survival between faithful and partner changed males) were similar for immigrants and residents. Resident males were slightly more likely to stay faithful to the partner between the subsequent breeding seasons, at any of the three stages of their breeding lifetime. Over the course of the study, fidelity rates of resident males were 0.79 (sd = 0.10), 0.76 (sd = 0.12), and 0.59 (sd = 0.13) for birds between their 2nd and 3^{d}, 3^{d} and 8th, and after 8th breeding season, respectively. For immigrant males the corresponding rates were 0.72 (sd = 0.14), 0.68 (sd = 0.14), 0.50 (sd = 0.14).

DISCUSSION

Patterns and drivers of pair fidelity are important to understand from both an evolutionary perspective, in terms of understanding the evolution of mating patterns, but also because of their potential influence on the population dynamics and viability of current populations. Fitness consequences of pair fidelity are usually addressed through the breeding success of a pair. Generally, breeding success increases over repeated breeding of a pair (e.g. Mills 1973, Black 2001, Naves et al. 2007) due to age related changes in breeding success (i.e. indirect effect) and benefits of ‘mate familiarity’ (Ens et al. 1993, Black 1996). In this study we built upon the knowledge of pair fidelity by using a novel probabilistic framework to address skipped breeding and survival consequences of pairing outcomes, as well as the influence of the previous pairing outcomes on the future ones. We also showed how fidelity rates, and fitness consequences of fidelity change with age and stage of breeding lifetime, and depend on the individual quality and immigration status.

Survival and breeding benefits of fidelity to a partner

We detected two important fitness benefits of pair fidelity in mute swans: the avoidance of skipped breeding, and increased survival. Although it was originally suggested that the costs of skipped breeding might be higher for short-lived species, where the future reproductive lifespan is short (McNamara and Forslund 1996), skipped breeding can also lead to substantial decrease in lifetime fitness even in long-lived species (Jouvetin and Bried 2001). While birds that keep their partners avoid the costs related to the search for a new partner (Choudhury 1995, Black 1996), birds that, for any reason, break up their partnership are exposed to different pressures, ranging from the competition to acquire a new partner, to reduced feeding and anti-predator activities. The cost should partly depend on the availability of potential partners, and should be lower in populations where there is surplus of non-breeders, or in colonial species (Bried et al. 2003, Jeschke and Kokko 2008). Our results indicate the existence of skipped breeding as one of the costs of partner change for birds that lose their partners even in a population where there is surplus of non-breeders (Perrins and McCleery 1994), and where coloniality might be thought to facilitate partner change. In addition, our finding that the cost of skipped breeding is higher for male than for female mute swans, and also higher for females at the beginning of their breeding lifetime (i.e. between 1st and 5th breeding season) than later, indicates that there might be different constraints to finding a new partner imposed on different sexes, and at different ages. For example, males might face stronger competition for partners, while younger females might be less dominant compared to older females. Our approach to infer skipped breeding from low recapture rates was additionally supported when we compared the fluctuation in our estimates of recapture rates to the estimated number of skipped breeders in the colony between 1981 and 1995 (Perrins and McCleery 1994). For the years when Perrins and McCleery (1994) estimated that there was a higher number of skipped breeders (individuals that bred at least once, but were not seen breeding in one or more seasons while being detected as alive in winter, or as breeding in later seasons), recapture rates obtained by our model were also lower.

Our study provides evidence that even in a long-lived species with a high survival rate, staying with the same partner might not only benefit breeding in terms of avoiding skipped breeding, but also through increased survival. Although variation in survival is one of the major components of fitness, it has rarely been addressed in studies of the effects of pair fidelity. While a few empirical studies have, indirectly, included a survival component by studying lifetime fitness of individuals, we are aware of only two studies that have directly addressed survival (Nicolai et al. 2012, Culina et al. 2013: Chapter 3). Culina et al. (2013) detected survival costs of partner change in short-lived great tits (*Parus major*), while Nicolai et al. (2012) showed that female black brants *Branta bernicla nigricans* that lost their partner in winter suffered reduced winter survival. In both of these species, pair members spend winter together (which is also thought to be the case in our swan population). Thus, associating with the partner might bring survival benefits through increased competitiveness of paired birds (Ekman 1990, Lemmon et al. 1997, Nicolai et al. 2012). Further support for this suggestion comes from our finding that survival benefits of staying faithful are higher for younger birds, which are likely to be of a lower social rank, and thus benefit more from association with the partner. More detailed observational data would be needed to understand the mechanisms behind the pattern.

Previous pairing outcomes predict future ones

Our finding that swans of both sexes that have already been faithful to their partner are more likely to stay faithful, compared to birds that have already changed a partner adds to the growing number of studies - in a range of contexts - that show how previous states can influence future ones (e.g. Peron et al. 2010, Sanz-Aguilar et al. 2011, Avril et al. 2012, Culina et al. 2013: Chapter 3). Our results also indicate that this trend reflects higher divorce (rather than widowing) rates of birds that had already changed partners compared to birds that had been faithful. Such an effect might be due to some birds being of lower quality, and being more likely to be left by their partner ('better choice' hypothesis, Choudhury 1995). However, we did not detect any overall differences in fidelity rates according to male quality (which we assumed to be approximated by their breeding longevity). Although we found that fidelity rates are different for female swans of different quality, this was more due to rates being different between the different stages of breeding lifetime, rather than at the overall level for different quality classes. On the other hand, the drop in fidelity rates we detected in older males, and in the final breeding seasons of long-lived females, are in line with the hypothesis that quality changes through individual lifetime, dropping at older ages (Auld et al. 2013); such an effect might lead to an increase in divorce rates. A further interesting possibility that might explain the influence of the current pair status on future pair status is that, once a bird changes partner (for any reason), low initial reproductive success with a new partner triggers further divorce (Culina et al. 2014: Chapter 2), and this continues in a cascade of events. Given the complex patterns of pair fidelity we detected, our results open several interesting possibilities to further study causes of this heterogeneity. One way to address these could be by using the same basic MECMR model, and extending it to incorporate breeding success by increasing number of possible states, or to memory models (Hestbeck et al. 1991, Rouan et al. 2009).

CONCLUSIONS

Our study of the pair fidelity rates and influence of fidelity on survival and skipped breeding in mute swans has three major findings. First, pairing outcomes (i.e. changing partner or staying with the same partner) can have a profound impact on individual fitness even in a long-lived species with high survival rates because they influence both survival and skipped breeding. Second, previous pairing outcomes can influence those in the future. Third, biased recapture rates, and uncertainty in state assignment must be taken into account when studying fidelity correlates (i.e. environmental, demographic, and individual level factors) and its fitness consequences, as it can greatly influence fidelity estimates, event in a species with relatively high recapture rates.

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SUPPLEMENTARY TABLES

Table S1. Summary of the approximate goodness-of-fit (GOF) test on the female mute swan dataset, for the two different types of models: time-dependent survival and recapture rate, time-dependent survival and recapture rate, with the immediate trap-dependence. The test of the fit for the models is composed of the Test2 (for trap-dependence) and the Test3 (for transience), The overall GOF test for the component Test2 and Test3 is calculated by removing the squared directional test statistics from the overall chi-squared of the Test2 and Test3. DF = degree of freedom; ĉ = the overdispersion coefficient calculated as the ratio between the chi-squared and the degree of freedom.

	Test2:trap-dependence		Test3: transience	
	χ2 - statistic	Squared directional statistics	χ2 - statistic	Squared directional statistics
Time-dependent model	305.23	203.63	66	0.48
DF	55	1	61	1
p-level	<0.001	<0.001	0.31	0.49
ĉ	5.54		1.08	
Time-dependent model with the heterogeneity in detection	101.60		65.52	
DF	54		60	
p-level	<0.001		0.29	
ĉ	1.88		1.09	

Table S2. Summary of the approximate goodness-of-fit (GOF) test on the male swan dataset, for the two different types of models: time-dependent survival and recapture rate, time-dependent survival and recapture rate, with the immediate trap-dependence. The test of the fit for the models is composed of the Test3 (for transience), and Test2 (for trap-dependence). The overall GOF test for the component Test2 of the model with the trap-dependence is calculated by removing the squared directional test statistics from the overall chi-squared of the Test2. DF = degree of freedom; ĉ = the overdispersion coefficient calculated as the ratio between the chi-squared and the degree of freedom.

	Test2:trap-dependence		Test3: transience	
	$\chi2$ - statistic	Squared directional statistics	$\chi2$ - statistic	Squared directional statistics
Time-dependent model	395.13	289.30	91.63	22.23
DF	52	1	62	1
p-level	<0.001	<0.001	0.01	<0.01
ĉ	5.54		1.48	
Time-dependent model with the heterogeneity in detection	105.83		69.4	
DF	51		61	
p-level	<0.001		0.25	
ĉ	2.08		1.14	

Table S3. Summary results of the multi-event mark–recapture analysis to estimate recapture, survival, and pair fidelity rates in female mute swans

		Model structure						
Parameter	recapture	survival	fidelity	np	dev	QAICc	Δi	w_i
recapture	age_R × state + t	age_C × state + t	age_R3 × state + t	125	9915.90	10175.05	0.00	1
	state			86	10055.50	10231.79	56.74	0
	age_R × state			92	10053.07	10241.99	66.94	0
	age_R + t			121	10072.73	10323.30	148.25	0
	age_R			88	10208.02	10388.52	213.47	0
survival	age_R × state + t	age_C × state + t	age_R3 × state + t	125	9915.90	10175.05	0.00	1
		age_C + t		120	9993.74	10242.17	67.11	0
		age_C		88	10137.40	10317.90	142.85	0
fidelity	age_R × state + t	age_C × state + t	age_R2 × state + t	122	9919.34	10163.34	0.00	0.81
			age_R3 × state + t	125	9915.90	10165.90	2.99	0.18
			age_R3 + t	122	10046.06	10290.06	126.71	0.00
			age_R3 × state	92	10122.78	10306.78	139.65	0.00

np = number of estimable parameters; dev = deviance; AICc = Akaike information criterion; Δi = the AICc difference between the current model and the model with the lowest AIC value; wi = Akaike weight;

state = state-dependent rates; c = constant rates; t = time-dependent rates; age = age-dependent rates where: age_C = chronological age (2 to 8 years old, or older); age_R = age since first capture (between 1st and 5th breeding season, or later); age_R2 = age since first capture (between 1st and 2nd breeding season, after 2nd breeding season); age_R3 = age since first capture (between 1st and 2nd breeding season, between 2nd and 8th breeding season, after 8th breeding season); + = additive effect of variables; × = interactive effect of variables.

Table S4. Summary results of the multi-event mark–recapture analysis to estimate recapture, survival, and pair fidelity rates in male mute swans

		Model structure						
Parameter	recapture	survival	fidelity	np	dev	QAICc	Δi	w_i
recapture	state + t	age_C × state + t	age_R3 × state + t	117	9727.05	9969.03	0.00	0.73
	age_R × state + t			119	9726.13	9972.38	3.35	0.14
	age_R + state + t			119	9726.18	9972.44	3.41	0.13
	age_R + t			118	10286.62	10530.74	561.71	0.00
survival	state + t	age_C × state + t	age_R3 × state + t	117	9727.05	9969.03	0.00	1.00
		age_C × state x t		175	9702.57	10070.66	101.64	0.00
		age_C + t		115	10068.82	10306.53	337.50	0.00
fidelity	state + t	age_C × state + t	age_R3 × state + t	117	9727.05	9969.03	0.00	0.99
			age_R2 × state + t	115	9740.41	9978.11	9.09	0.01
			age_R3 + state + t	115	9878.02	10115.73	146.70	0.00

The notation is the same as in the Table S1.

S5. Summary results of the multi-event mark–recapture analyses on pair fidelity rates according to breeding longevity of female and male mute swans (using separate datasets for each sex). The structure of the recapture and survival part of the models is always ‘state + t’ for recapture, and ‘t + state x age2’ for survival.

Dataset	fidelity	np	dev	QAICc	Δi	w_i
Females	longevity × age1 × state + t	127	4485.93	4757.29	0.00	0.99
	longevity × age1 + t	107	4572.84	4799.05	41.76	0.00
	age1 × state + t	98	4672.98	4879.18	206.20	0.00
	age3 × state + t	85	4780.68	4958.26	200.97	0.00
Males	age2 × state + t	90	5283.44	5471.30	0.00	0.99
	age3 × state + t	84	5305.53	5480.37	9.07	0.01
	age1 × state + t	102	5270.94	5485.09	13.79	0.00
	longevity × age2 × state + t	127	5298.31	5568.21	96.91	0.00
	longevity × age2 + t	107	5395.22	5620.41	149.11	0.00

*The notation same as in the Table S1, except:

age1 = rates differ for each pair of the subsequent breeding seasons(from the 1st to the 11th breeding season); age2 = rates differ between 1st and 2nd breeding season, between 2nd and 3d; between 3d and 7th, between 8th and 10th, and after; age3 = rates differ between 1st and 2nd breeding season, after 2nd breeding season; longevity = breeding longevity of individual: 1 year, 2 years, 3-4 years, 5-6 years, 7-10 years, 11 years or longer

Table S6. Summary results of the multi-event mark–recapture analysis on the influence of immigration status on recapture, survival, and pair fidelity rates in female mute swans.

recapture	survival	fidelity	np	dev	QAICc	Δi	w_i
age_R + state + t	age_s × state × im_status + t	age_s × state + t	101	4599.06	4811.95	0.00	0.26
age_R + state × im_status + t	age_s × state × im_status + t	age_s × state + t	103	4594.85	4812.19	0.24	0.23
age_R + state × im_status + t	age_s × state × im_status + t	age_s × state + im_status + t	104	4593.33	4812.95	1.00	0.16
age_R + state + t	age_s × state × im_status + t	age_s × state + im_status + t	102	4597.72	4812.84	0.88	0.04
age_R + state × im_status + t	age_s × state + im_status + t	age_s × state+t	95	4616.13	4815.75	3.79	0.02
age_R + state × im_status + t	age_s × state + im_status + t	age_s × state + im_status + t	96	4615.31	4817.14	5.18	0.00
age_R + state + t	age_s × state + t	age_s × state × im_status + t	101	4619.29	4832.18	20.23	0.00
age_R + state × im_status + t	age_s × state + t	age_s × state × im_status + t	103	4619.13	4836.47	24.51	0.00
age_R + state + t	age_s × state + t	age_s × state+t	92	4645.20	4838.21	26.25	0.00
age_R + state × im_status + t	age_s × state + t	age_s × state+t	94	4642.97	4840.38	28.43	0.00

The notation is the same as in the Table S1, except:

age_s = age since first recapture-dependent rates, rates differ between 1st and 2nd breeding season, between 2nd and 3d; between 3d and 7th, between 8th and 10th, and after; im_status = immigration status (immigrant or resident) dependent rates.

Table S7. Summary results of the multi-event mark–recapture analysis on the influence of immigration status on recapture, survival, and pair fidelity rates in male mute swans.

recapture	survival	fidelity	np	dev	QAICc	Δi	w_i
age_R + state + t	age_s × state + im_status + t	age_s × state + im_status + t	94	4862.84	5060.10	0.00	0.75
age_R + state × im_status + t	age_s × state + im_status + t	age_s × state + im_status + t	96	4861.73	5063.39	3.29	0.14
age_R + state + t	age_s × state + im_status + t	age_s × state + t	93	4869.58	5064.64	4.54	0.08
state + t	age_s × state × im_status + t	age_s × state + t	99	4859.81	5068.11	8.01	0.01
state × imm_status + t	age_s × state × im_status + t	age_s × state + t	101	4858.72	5071.44	11.35	0.00
state + t	age_s × state + t	age_s × state + t	90	4884.82	5073.30	13.20	0.00
state × im_status + t	age_s × state + t	age_s × state + t	92	4883.08	5075.95	15.85	0.00
state + t	age_s × state + t	age_s × state × imm_status + t	99	4870.42	5078.71	18.61	0.00
state × im_status + t	age_s × state + t	age_s × state × imm_status + t	101	4867.82	5080.54	20.44	0.00
state × im_status + t	age_s × state × im_status + t	age_s × state × imm_status + t	110	4851.87	5084.64	24.54	0.00

The notation is the same as in the Table

CHAPTER 6

Carry-over effects of the social environment on future divorce probability in great tits

Carry-over effects of the social environment on future divorce probability in great tits

Antica Culina, Camilla Hinde, and Ben C. Sheldon

ABSTRACT

1. Both initial mate choice and re-mating strategies (infidelity and divorce) can have a big impact on individual fitness. Both may be influenced by the social environment, which determines the number and availability of potential partners.

2. Most studies of the influence of the social environment on mating strategies take a population-level approach; hence, individual-level responses to variation in the social environment remain largely unexplored.

3. In this study we aim to better understand the influence of the social environment in which a pair has formed on later divorce. Using detailed data on winter social networks of tagged birds we tested whether the divorce probability of a pair of wild great tits can be predicted by the number of associates of the opposite sex (between-sex degree), the rank of the future partner amongst these associates, and the association strength between the pair members in the winter prior to the first breeding of a pair.

4. We found that males with a higher between-sex degree, and males whose partner ranked lower amongst their female associates before breeding were more likely to divorce after breeding. We did not find any evidence that a female's social environment influenced divorce probability.

5. Our findings highlight the importance of the immediate social environment individuals experience during pair formation to later pairing outcomes. Exploring these extended

effects of the social environment can give valuable insights into processes and selective pressures acting upon the mating strategies that individuals adopt.

INTRODUCTION

The social environment has repeatedly been shown to shape individual fitness, population dynamics, and selection acting on behavioural and morphological traits, not only in humans (Smith et al. 2001, Kameda and Nakanishi 2003, Apicella et al. 2012), but also in other animals (McDonald 2007, Ryder et al. 2009, Oh and Badyaev 2010, Kurvers et al. 2014). One of the main pathways for these effects is via the influence of the social environment on reproductive success. For example, Oh and Badyaev (2010) found that male house finches (*Carpodacus mexicanus*) with non-elaborated plumage (which are less preferred by females) can increase their mating success if they change winter flocks often (thus changing selection on ornamentation). Social effects need not be immediate, but may have extended fitness consequences, even several years after the interactions have happened. For example, the connectivity of young long-tailed manakin (*Chiroxiphia linearis*) males with other males in their social network predicted both their social rise and mating success up to 8 years afterwards (McDonald 2007). The social environment should be especially important for primary (i.e. the initial mate choice) and secondary (i.e. divorce and infidelity) mating strategies in socially monogamous species where mate sampling might be limited and hence constrained by the social environment; such constraints might lead to the formation of a suboptimal partnership (Bateson and Healy 2005).

Suboptimal partnerships in socially monogamous species can be adjusted either by mating outside of the social pair (i.e. infidelity) and/or by divorcing a partner after the initial breeding (Choudhury 1995, Black 1996, Petrie and Kempenaers 1998, Griffith et al. 2002). Consequently, when the social environment influences initial mate choice by determining the number of opposite-sex associates (Ens et al. 1993, McNamara et al. 1999, Maxin and Berec 2010), it should also influence the emergence of the secondary mating strategies. In this way, the social environment may not only impact breeding success through the immediate effects of the quality of the social partnership, but also through later fitness effects of secondary mating strategies. For example, across socially monogamous birds, divorce has been shown to lead to an increase in reproductive success, if divorced individuals survive to breed, with a new partner (Culina et al. 2014: Chapter 2).

However, the social environments of individuals, and their subsequent effects, are challenging to study because they require detailed knowledge on the behaviour of individuals. In free-ranging animal populations data on the social environment are difficult and time-consuming to obtain. Consequently, studies often use a range of demographic proxies, such as sex ratio, coloniality, or mortality rates as an estimate of social environment individuals are exposed to (Dubois et al. 1998, Jeschke and Kokko 2008, Liker et al. 2014). For example in their recent phylogenetic comparative analysis, Liker et al. (2014) showed that divorce rates are higher in species with a female-biased adult sex ratio. While these studies have given valuable insights into the ways demographic factors influence divorce rates, responses to the immediate social environment at the individual level have received less attention. Moreover, studies using large-scale demographic factors do not distinguish between the demography of the environment in which a pair had formed (i.e. before the first breeding), and of the environment in which divorce has happened (i.e. after the first breeding). Advances in the application of social network theory to study heterogeneous associations within animal groups, along with the developments of new tracking technologies, have enabled easier, more straight forward, and statistically more robust descriptions of the social environment that individuals are exposed to, as well as differences in the social interactions that individuals exhibit (reviewed in Croft et al. 2008, Sih et al. 2009; Garroway et al. 2014).

In this study we use novel tracking techniques to construct social networks in winter flocks of great tits (*Parus major*) and to test whether components of the social environment in the winter prior to the first breeding of a pair can predict its future divorce probability after breeding. The main predictions we tested were: (i) birds that had fewer associates of the opposite sex in the winter prior to the breeding season *t* would divorce more often between breeding seasons *t* and *t*+1. We reasoned that a smaller number of opposite-sex associates would restrict the pool of potential partners from which to sample and to choose from. This should increase the incidence of suboptimal partnerships, and lead to higher divorce probability later; (ii) birds with weaker preference (measured in terms of the strength of association) with their future partner would divorce more often between breeding seasons *t* and *t*+1. We reasoned that a lower association strength and lower partner rank should indicate a low preference for that partner (in comparison to other birds of the opposite sex).

MATERIALS AND METHODS

Great tits

Great tits breed in socially monogamous, territorial pairs, and spend the winter in mixed species flocks composed of variable numbers of individuals (Gosler 1993). Although the great tit is one of the most commonly studied bird species, knowledge about the process of pair formation, winter social behaviour and its influence on the pairing outcomes is still very sparse (Gosler 1993). Previous studies indicated that breeding pairs generally form between birds belonging to the same core winter flock (Hinde 1952, Bjorklund et al. 1989), mostly after the winter flocks dissolve, but also while still a part of the flock (Hinde 1952, Saitou 1979). However, more recent work has demonstrated that pairs do form throughout the winter, with possibly several peak periods of pair formation, depending on the winter (Chapter 7, this Thesis). Reported divorce rates in great tits vary between 0-51% (e.g. Dhondt et al. 1996). Divorce in great tits sometimes follows breeding attempts with low breeding success (Perrins and McCleery 1985, Szulkin and Sheldon 2008), and happens more often in pairs containing first year breeders (i.e. birds between their first and second breeding season, Saitou 2002, Pampus et al. 2005). Two studies have suggested that social organisation in winter and winter residency might influence divorce probability in great tits (Dhondt et al. 1996, Saitou 2002). Both of these studies concentrated on divorce in relation to whether pair members spent winter in the same flock or not, after they had already bred. Dhondt et al. (1996) found that divorce occurred more often in populations with lower winter residency. On the other hand, Saitou (2002) did more detailed observations of flocks of colour-ringed birds. He found that divorce happened more often in pairs that, after breeding together, belonged to different winter flocks, but also in pairs that belonged to different flocks before breeding. However, more detailed data on fine-scale social influences on divorce, as well as more studies on winter social behaviour and divorce in great tits to explore the generality of these findings are still needed.

Data collection and construction of social networks

We collected data on winter flocks (2007 to 2009 winters, and 2011 winter) and breeding pairs (2008 to 2013 breeding seasons) of a free-ranging great tit population in Wytham Woods (51° 46’ N, 1° 19’ W). We needed data on winter flocks in the winter of pair formation (i.e. winter prior to the breeding season *t*) to explore the influences of the social environment in that winter on the probability of a pair to divorce between breeding seasons *t* and *t*+1 (e.g. data on 2011 winter were used to explore influences on divorce between 2012 and 2013 breeding seasons). Data on winter flocks were collected using radio-frequency identifiacation (RFID) technology to detect birds marked with pasive integrated transporders (PIT-tags) while they feed at feeders equipped with PIT-detecting antennae. Birds received PIT-tags when first ringed, either as breeders or nestlings during the standardised monitoring of the breeding population (Perrins 1965, Perrins 1979, Gosler 1993), or when captured during constant winter catching (mostly immigrants). This ensured that the majority of birds wintering in the woods were tagged (more than 80% of birds, Matechou et al. in press). Tagged birds were registered at an array of logger-equipped feeders placed at different feeding locations. During winters 2007 to 2009, 16 (out of overall 67) feeders were open (and thus available for birds) at any time between August and March. These were rotated every four days around 67 feeding locations following a structured randomised design, so that each of 8 approximately equally-sized sections of the woods always had two active loggers in it. In the 2011 winter there were 65 feeders, all of which were simultaneously opened once a week, for two subsequent days (weekends), between the beginning of December and the beginning of March. The data-collection set up reduced the possibility that flocks would get attracted to the constant food source, and we assume that data gathered at feeders represent a 'snapshot' of the social composition at the time of feeding. Data on breeding pairs (i.e. identities of pair members and details of their breeding parameters) were collected using standardised protocols (Perrins 1965, Perrins 1979, Gosler 1993). We used this information to determine the incidence of pair fidliety (i.e. pairs that breed together in the year *t* and again in the year *t+1*), and divorce (i.e. pairs that bred in the year *t*, where both members survive to the next season, but breed with different partners in the year *t*+1).

We based the construction of social networks on the spatio-temporal detection of co-occurrence of individuals at feeders (i.e. gambit of the group approach, Franks et al. 2010). We used the GMMEvent (Gaussian mixture model for event streams) method (Psorakis et al. 2012) to extract association matrices from the data collected on loggers. In the first three winters these matrices were constructed for each month, and for the 2011 winter for each weekend of the data collection. We excluded those birds that were first detected in February (2007 to 2009 winters) or in the last two weekends of data collection (the 2011 winter). For each winter, we calculated the degree (the number of individuals the focal birds was associated with) and between-sex degree (the number of the opposite sex individuals the focal bird was associated with). Degree and between-sex degree were strongly correlated in both datasets and in both sexes (males: Kendall's $\text{tau}_{(2007\text{to}09)} = 0.82$, $p<0.001$; $\text{tau}_{(2011)} = 0.89$, $p<0.001$; females: $\text{tau}_{(2007\text{to}09)} = 0.95$, $p<0.001$, $\text{tau}_{(2011)} = 0.86$, $p<0.001$). We used between-sex degree for our analysis as it better reflects the number of the opposite sex associates. We calculated the strength of the association between the two individuals (i.e. between males and females) using the half weight index (Cairns and Schwager 1987, Whitehead 2008). We scored partner rank using the following procedure: first, we calculated the association strength between the focal bird and each bird of the opposite sex (including its future breeding partner) that the focal bird associated with; second, we ordered these from the highest to the lowest; third, we determined the placement (i.e. the rank) of the focal bird's breeding partner on the list. For example, if the future partner rank is 1, this means that, considering all opposite sex associations, the focal bird associated most strongly with its future partner. We provide the frequency distribution of partner strength, female's and male's partner rank, female and male between-sex degree, for winters 2007 – 2009, and for the winter 2011 in the Supplement (Figs S1&2).

Data analysis

To test for the influence of social network traits in the winter of pair formation (i.e. winter prior to the breeding season *t*) on the probability of a pair to divorce between breeding seasons *t* and *t*+1, we considered newly formed pairs (i.e. pairs that formed in the winter prior to the breeding season *t*). This required that both pair members were tagged in the winter prior to the breeding season *t*, and that both survived between *t* and *t*+1 breeding seasons. Subsequently, sample sizes (especially for the first three winters of data collection) were reduced despite the large number of birds studied (Table 1). Because we were interested in the absolute number of associates of the opposite sex (i.e. the pool of the potential breeding partners), the effect of which should be independent of winter, we combined the first three winters into one dataset (to increase the sample size), and kept the 2011 winter as the other (because the methods used were different). Similarly, partner rank indicates the preference of the focal bird to associate with its partner, even if winters differ in the distribution of association strengths amongst all birds, and should thus be independent of winter too. On the other hand, the association strength between the future pair members is more likely to relate to winter specific effects (i.e. if the distribution of association strength differs between different winters). Thus, we checked whether winter had a strong influence on the association strength between pair members (including all pairs in the network, and not only the newly formed pairs). We compared the AIC values (Anderson and Burnham 2002) of the two simple linear models with the association strength as the response, and with or without (i.e. the intercept model) winter as the explanatory variable. These two models gained similar support ($AIC_{no\ winter} = -73.69$, $AIC_{winter} = -69.61$, LR test P=0.59), further justifying the treatment of the first three winters as one dataset.

Table 1. The number of pairs, breeding together for the first time in the breeding season *t*, for which both partners were detected in the winter prior to *t*, and where both survived to season *t*+1 to either breed together (fidelity) or with a new partner (divorce). Status refers to the pair status in *t*+1 (divorced or faithful). However, in some of these pairs the pair members were never detected to be associated (given in brackets) and these pairs were not included in the main model selection. Winter refers to the winter prior to the breeding season *t*. For example, out of 6 pairs that formed in the winter of 2007 (and bred for the first time in 2008 breeding season), 3 divorced, and 3 remained faithful to the 2009 breeding season.

Status	Winter	2007	2008	2009	2011
Divorced		**3 (0)**	**3 (0)**	**0**	**8 (3)**
Faithful		**3 (3)**	**9 (3)**	**3 (1)**	**23 (7)**

We ran the binomial glm's, with pair status in *t*+1 as a binomial response variable (divorced or faithful) to test for the variables influencing divorce probability. We considered five main explanatory variables (that describe the social environment and the preference for the partner), and two control variables in our models:

i. main explanatory variables: partner strength, male between-sex degree, male's partner rank, female between-sex degree, female's partner rank (all of these calculated in the winter before the breeding season *t*);

ii. control variables: data collection method (2 possible values: winter 2007 - 2009, or 2011), and clutch size.

We compared the performance of nine competing models (Table 2), for each sex separately, including three main explanatory variables (for males this was partner strength, male between-sex degree, and male's partner rank; for females this was partner strength, female between-sex degree, and female's partner rank and two-way interactions between partner strength and male's (or female's) partner rank, and partner strength and male (or female) between-sex degree. Because some members of the future pairs were never detected in the same winter flock (i.e. associated), we restricted the main analysis to only those pairs that were detected in the same flock at least once. This was necessary as partner strength and partner rank can only be estimated for those pairs that were seen associated. In addition, we have used the full dataset (i.e. including all new pairs) to test for the influence of male between-sex degree on the divorce probability. We also checked if pairs never seen associated in winter were more likely to divorce, but did not find any support for this (AIC of model, controlled for clutch size and winter, was similar in model with: AIC = 68.43; and without: AIC = 66.43 the variable coding for whether a pair was ever seen together or not). We controlled for both control variables in each model. We have shown (Chapter 7, this thesis) that clutch size is an important predictor of divorce in great tits and closely related tit species. We considered the model with the lowest AIC value as the best supported one if this value was 3 or more units lower than the AIC of the next lowest AIC model. In addition to the main set of models, we also ran all the models (i.e. 1-9, Table 2) with the proportion of same-sex associates as a measure of the intensity of the competition for partners. We added the proportion of same-sex associates as an additive effect to the main model structure, or replaced between-sex degree with the proportion of same-sex associates (Supplementary Table S1 for males, Table S2 for females).

RESULTS

Model selection on the social correlates of divorce probability of newly formed pairs of great tits (Table 2) gave the best support to the model with male's between-sex degree, male's partner rank, partner strength, and the interaction between the last two (coefficient estimate for the interaction term = 18.94, SE = 9.97, z-value = 1.89, p = 0.05). However, the support for the model without male between-sex degree was only slightly better than for the model with male's partner rank and male's partner strength only. The divorce probability of a newly formed pair increased with the number of female associates a male had (i.e. male between-sex degree) in the winter of pair formation (Fig 1a). Divorce probability also increased with the decrease in rank of a female on the list of male's female associates (Fig 1b). The probability that a male with the lowest number of female associates (which was 12) in winters 2007, 2008 and 2009 would divorce to the next breeding season (i.e. between 2008 and 2009 breeding season, between 2009 and 2010, and between 2010 and 2011, respectively) was 0.55 (95% CI = 0.1–0.9). This probability increased to 0.99 (95% CI = 0.37–0.99) for a male with the highest number of female associates (77). In the 2011 winter the pattern was even more pronounced, with divorce probability increasing from 0.03 (95% CI = 0.001–0.45) for males of the lowest between-sex degree, to 0.81 (95%CI = 0.20–0.99) for males of the highest between-sex degree (Fig 1a). The divorce probability ranged between 0.19 (95% CI = 0.04–0.57) for males whose breeding partners ranked 1st amongst all the female associates in winters 2007, 2008, and 2009, and 1 (95% CI = 0.85–1) for males whose females ranked as 14th (Fig 1b). In the 2011 winter, the probability ranged between 0 (95% CI = 0–0.2) and 1 (95% CI = 0.62–1). Finally, there was an interesting interaction between partner rank and partner strength. While males whose partner was ranked as their 1st female associate had the same (and low) probability of divorcing that partner, for males whose partner was ranked lower amongst their female associates, the divorce probability increased with the increase in partner strength (Fig 2a&b). We did not find support for models where the proportion of male associates within all of the male's associates influenced the future divorce probability of a pair (Supplementary Table S1).

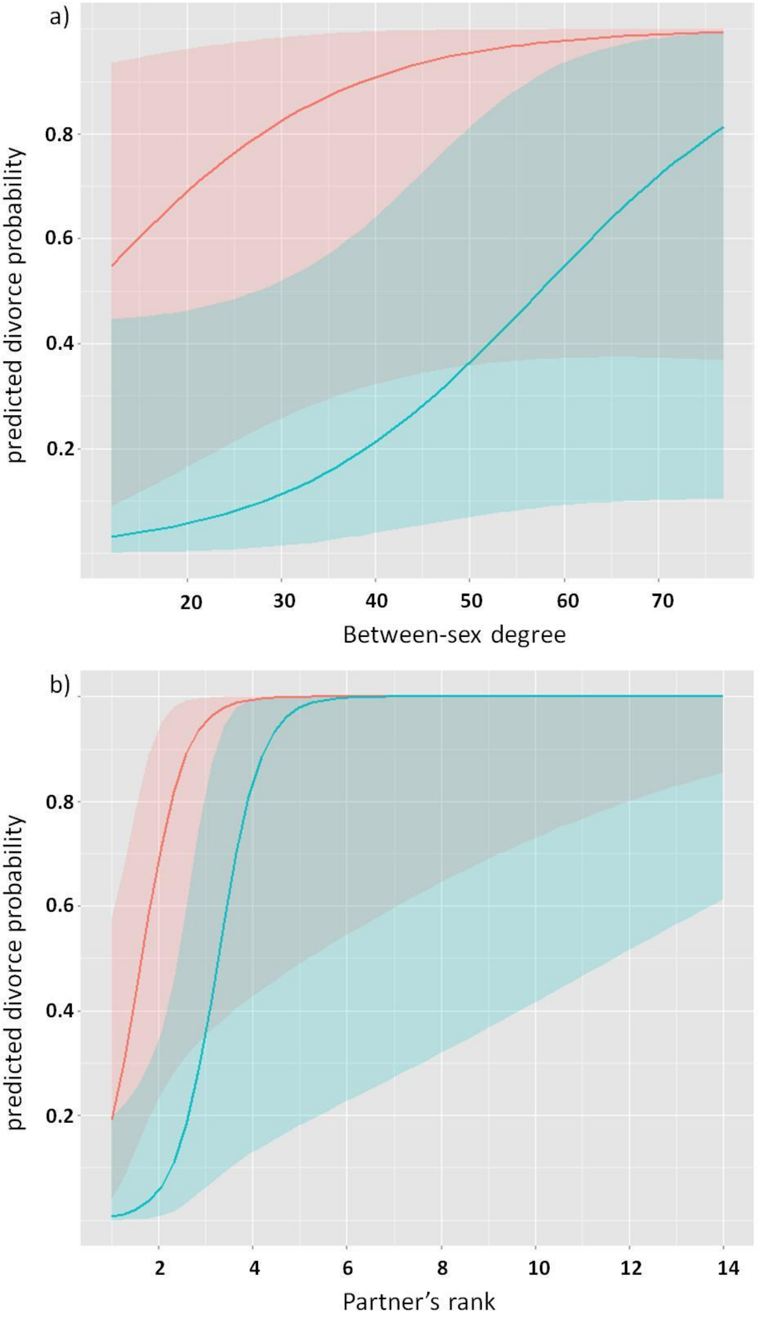

Figure 1. The predicted probability of a newly formed great tit pair (breeding in the season *t*) divorcing (as opposed to staying faithful) between breeding seasons *t* and *t*+1 (as obtained by the best binomial glm, controlling for the effect of the clutch size of a pair) according to a) male's between-sex degree (number of the opposite sex associates); and b) rank of male's partner (given the association strength) amongst all of his opposite sex associates (rank 1 is the female bird with whom the male has the strongest association), in the winter prior to the breeding season *t*. Results are given for two sets of winters (red = winters 2007 to 2009; blue = winter 2011).

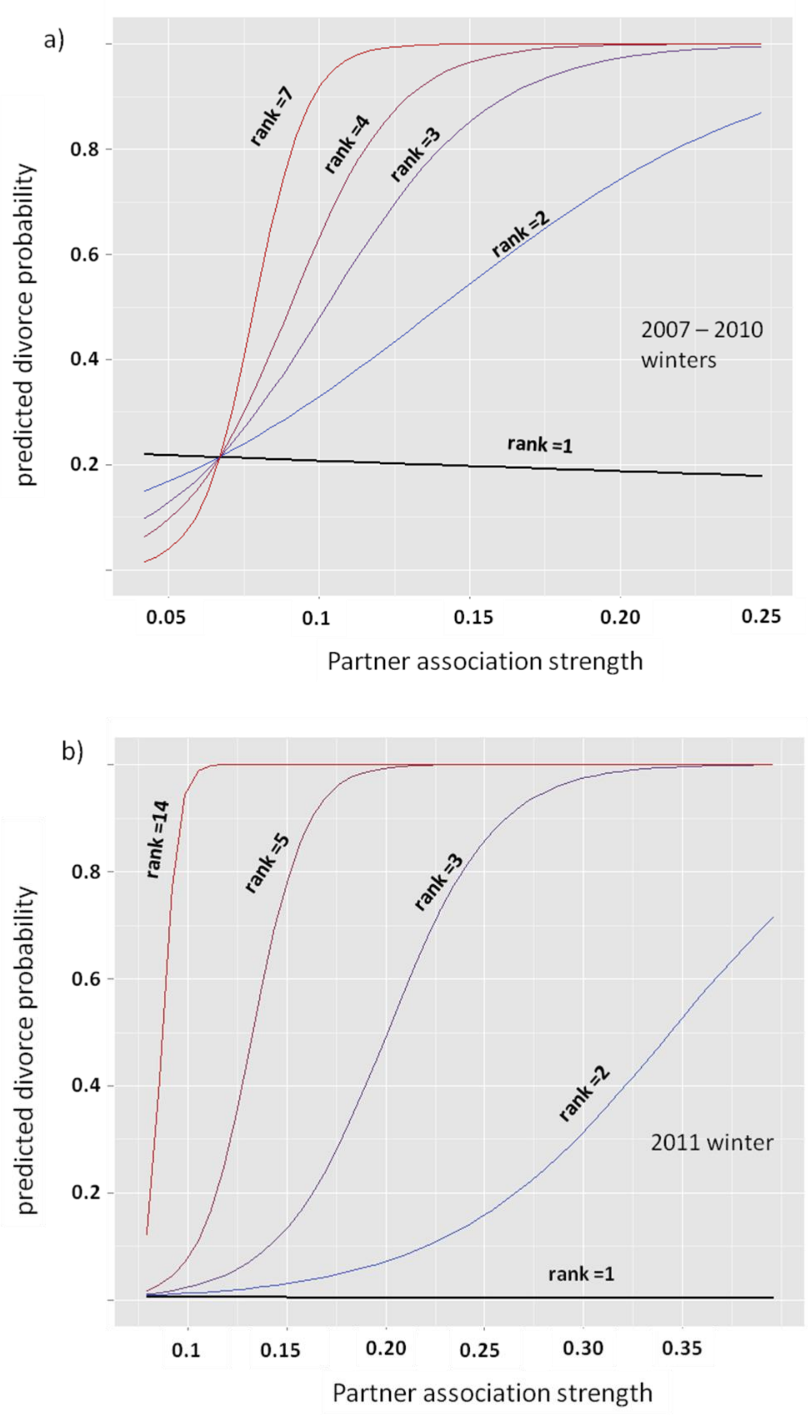

Figure 2. The predicted probability of a newly formed great tit pair (breeding in the season *t*) to divorcing (as opposite of stay faithful) between breeding seasons *t* and *t*+1 (as obtained by the best binomial glm, controlling for the effect of the clutch size of a pair) according to association strength between pair members and rank of male's partner (given the association strength) amongst all of his opposite sex associates (rank 1 is the female bird with whom the male has the strongest association), in the winter prior to the breeding season *t* in two sets of winters a) winters 2007 to 2009 b) winter 2011.

Our additional analysis, using all males of newly formed pairs (and not just those that were seen associated with their future females) also gave best support to the model where male's between-sex degree influenced the future divorce probability of a pair (Table S4). Estimated divorce probabilities were similar to the previous ones, however, with the narrower 95% CI (probably due to larger sample size). For the first three winters males with the lowest (this was 1) between-sex degree had 0.08 (95% CI = 0.01–0.35), and males with the highest (this was 78) between-sex degree 0.75 (95% CI = 0.29–0.96). In the 2011, corresponding probabilities were 0.04 (95% CI = 0.00–0.29), and 0.56 (0.23–0.85).

We found no support that female between-sex degree or female's partner rank influenced divorce probability (See, Supplementary Table S3 for model selection, for some combinations of explanatory variables it was not possible to fit the models). We also did not find support for models where the proportion of female associates within all of the female's associates influenced the future divorce probability of a pair (Supplementary Table S2). Finally, the additional analysis, using all females of newly formed pairs (and not just those that were seen associated with their future males) did not give any support to the models where female's between-sex degree influenced the future divorce probability of a pair (Table S5).

Table 2. The 9 main models (with the support and the corresponding statistic for each) used to test for the possible influence of males between-sex degree, partner strength, and male's partner rank (i.e. how high a male's breeding partner is on the list of all of his female 'friends') in the winter prior to the first breeding of a pair (i.e. winter in which a pair has formed) on the divorce probability of a pair to the next year. We controlled for winter (two levels: 2007-2009; and 2011), and the clutch size of the pair in all models. All models were run as binomial glms in R.

Model structure (always including + clutch + winter)	AIC	Null deviance (df)	Residual deviance (df)
partner strength x m partner rank + m between degree	37.40	40.49 (35)	23.40 (29)
partner strength x m partner rank + m between sex degree x m partner rank	39.20	40.49 (35)	23.20 (28)
partner strength x m partner rank	39.21	40.49 (35)	27.21 (30)
m partner rank + m between degree	43.80	40.49 (35)	33.80 (31)
m between degree	42.11	40.49 (35)	34.11 (32)
partner strength + m between degree	43.92	40.49 (35)	33.92 (31)
partner strength	44.96	40.49 (35))	36.96 (32)
-	44.57	40.49 (35)	38.57 (33)
partner strength + m partner rank + m between degree	45.78	40.49 (35)	33.78 (30)

DISCUSSION

In this study we used a detailed dataset of associations between males and females in winter flocks of wild great tits to describe the number of the opposite-sex associates, and the preference of males and females to associate with their future breeding partners. Our results showed that the males' social environment (but not the females') and the preference to associate with his future breeding female influenced the divorce probability of a newly formed pair. Males with more female associates, and males who had their breeding partner ranked relatively low amongst these, had a higher divorce probability after the next breeding season. Previous studies on the influence of the social environment (approximated through demographic factors) on divorce probability have not looked at the social environment in which a pair has formed. Our findings should be considered from the three main perspectives: 1) the importance of the social environment (in terms of the possible mating options) in mate choice; 2) males as a sex that exhibits partner preferences; 3) the extended influence of the social environment in which mate choice takes place on future fitness.

The influence of the social environment on mate choice decisions has most often been studied in the context of non-independent mate choice (commonly mate choice copying, Westneat et al. 2000), and the relative attractiveness of a male compared to his associates (e.g. Bateson and Healy 2005, Oh and Badyaev 2010a, Callander et al. 2011). Both empirical and theoretical work on these two aspects has emphasised that social influences on mate choice might have a substantial impact on sexual selection (Westneat et al. 2000, Bateson and Healy 2005). The third aspect of the social influence on mate choice is the number (and quality) of possible partners to choose from (Shuster and Wade 2003). For example, the frequency of extra-pair fertilisations in a house finch population was found to be largely determined by the availability of suitable extra-pair mates (Lindstedt et al. 2007), and is thus specific for each individual in the population. Our study demonstrates that divorce, which can be considered as a form of mate choice (Black 1996), and a way to correct for a suboptimal mating situation (Culina et al. 2014:

Chapter 2), might also depend on some aspects of the social environment in which initial mate choice happens. Interestingly, our finding that males with more female associates during the period of pair formation divorced more often after breeding was opposite to our prediction (i.e. we expected that a larger number of opposite-sex associates would enable sampling more prospective partners, and thus leads to a better initial mate choice and lower divorce probability later). This was not related to the intensity of competition (which we expressed as a percentage of the same sex associates), where high intensity may limit the possibilities available for preferred pairing regardless of how many females a male associates with. One possible explanation for the observed effect comes from the theoretical model of the stable matching of pairs. Hills and Todd (2008) have modelled the stability of pairs as a function of population heterogeneity in a quality trait, and found that in populations with the higher heterogeneity stable matching between males and females became less frequent. Thus, if males associating with more females also experience higher heterogeneity of mating options, they might make less stable mating choices. However, there are other explanations, such as the possibility of the correlation between personality, social behaviour (Aplin et al. 2013), and divorce probability. Our result that even males that were never seen associating with their partner in winter still divorced more often if they had more female associates is in accordance with this later possibility. More detailed analysis of the composition of flocks and the way the composition changes over winter could help to reveal the mechanism behind our findings.

Although mate preferences have traditionally been studied in females (Andersson 1994, Westneat et al. 2000) there is increasing evidence that males might be choosy (Clutton-Brock 2009), especially in social monogamous species where both parents care for offspring (Johnstone et al. 1996). Results of some studies indicate that divorce, as a type of a secondary mate choice, could also be driven by both sexes (Cezilly et al. 2000). For example, while divorce seems to be female driven in black-capped chickadees, *Poecile atricapillus*, where females abandon their partner for a male of higher quality, it is thought to be driven by males in house wrens, *Troglodytes aedon* (Poirier et al. 2003). Our result that male's but not female's preference for the future breeding partner (expressed as a partner rank) influenced the probability of a pair to divorce after their first breeding, indicates that males likely use divorce to correct for non-preferred partnerships. Low female rank on the list of his female associates most likely reflects the situation where male was not able (because of the competition or/and female choice) to breed with his preferred female, and ended up breeding with a less preferred one. Interestingly, while low partner rank was related to the high divorce probability in both sets of winters, males that had their partners ranked high were more likely to divorce in the first three years than in the final year. This could likely be connected to the difference in the start of data collection, and to the time periods when majority of future pairs start associating, and thus expressing partner preferences (see Chapter 7, this thesis). Exploring finer temporal changes in its partner rank, and keeping the track of the most preferred female over time would be a good way to study the observed pattern in more detail.

Finally, a growing number of studies show that social experiences might have an extended influence on individual fitness (McDonald 2007, Gersick et al. 2012, Stanton and Mann 2012, Gilby et al. 2013). For example, juvenile males zebra finches (*Taeniopygia guttata*) that were placed to grow up with a single female showed more intense courtship, aggressiveness, and were more attractive to females later in life than were males reared in mixed-sex groups (Ruploh et al. 2013). Because breeding success (Black 1996, Culina et al. 2014: Chapter 2), and even survival (Nicolai et al. 2012, Culina et al. 2013: Chapter 3), can be affected by fidelity to a partner and partner change in monogamous birds, the social environment thus has a potential to influence the overall fitness not just through initial mate choice, but also through later mating outcomes. Moreover, divorce and fidelity have the potential to influence overall population dynamics and productivity (Berec and Boukal 2004, Maxin and Berec 2010), as well as the intensity of the sexual selection operating on individual traits (DuVal 2013).

CONCLUSIONS

Our study demonstrates that divorce in monogamous species might not only be affected by the social environment to which existing pairs are exposed, but also by the social environment in which pairs have formed. This environment is likely to constrain the initial mate choice, subsequently shaping secondary mating strategies individuals adopt. At the same time our results also indicate that, at least in this study, this might be more driven by the male's social environment and preference for a partner than by the female's. Further exploration of these carry-over effects of the social environment, and how they differ between males and females, might give new valuable insights into processes of mate choice, population dynamics, and sexual selection.

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SUPPLEMENTARY FIGURES

Figure S1. Frequency distribution of 5 main explanatory variables (association strength between pair members, female and male between-sex degree, female's and male's partner rank in the winter of pair formation) we used to model the probability of a newly formed great tit pair to divorce later. Data are given for 2007, 2008, and 2009 winters combined.

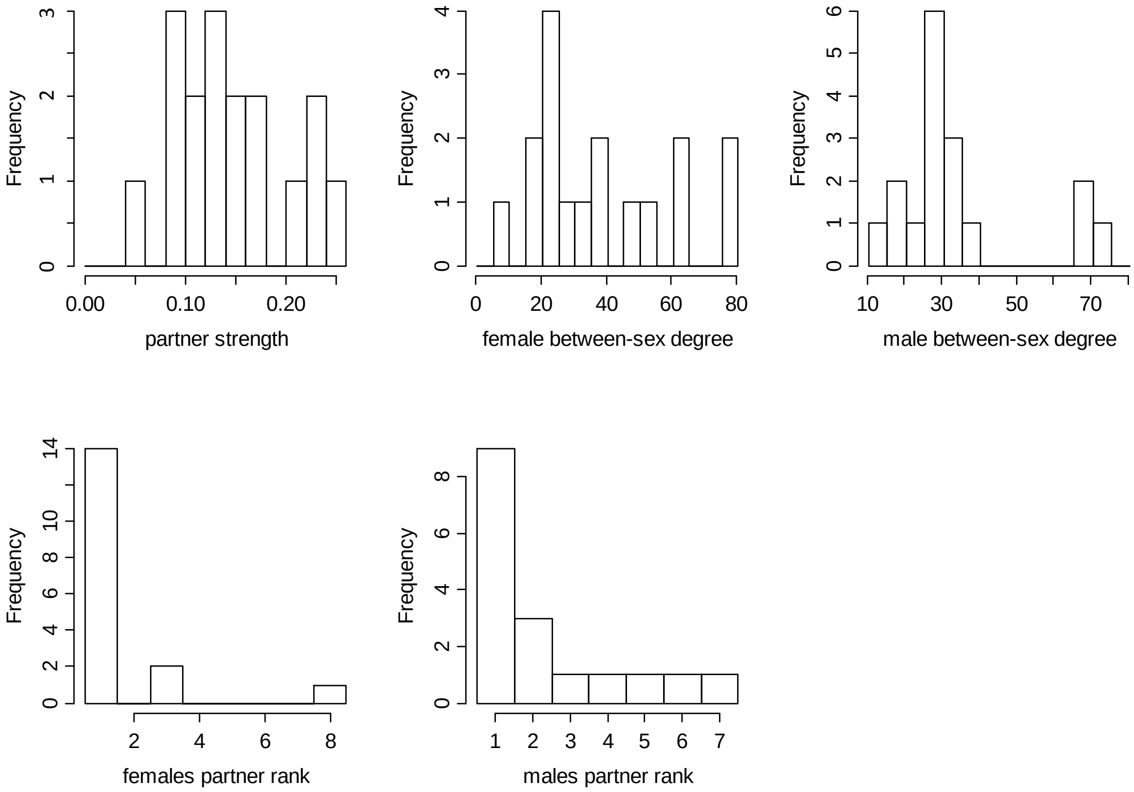
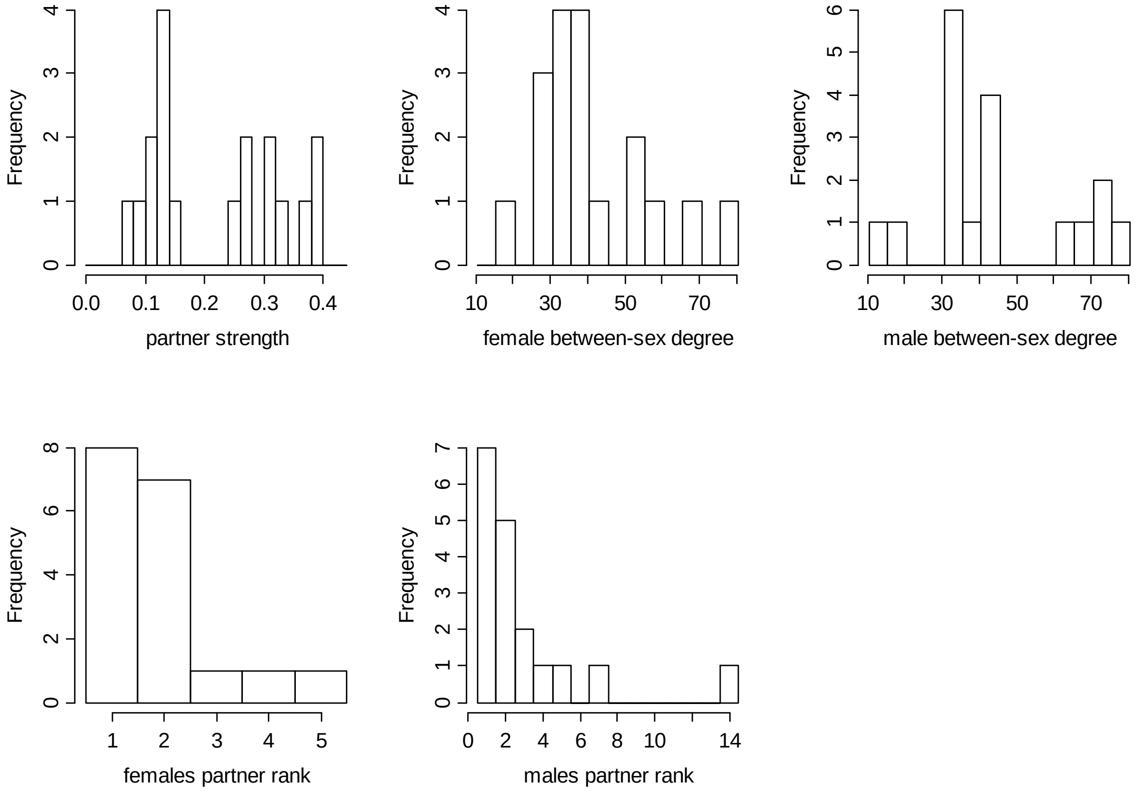


Figure S2. Frequency distribution of 5 main explanatory variables (association strength between pair members, female and male between-sex degree, female's and male's partner rank in the winter of pair formation) we used to model the probability of a newly formed great tit pair to divorce later. Data are given for 2011 winter.



SUPPLEMENTARY TABLES

Table S1. 12 models (with support and the corresponding statistic for each) we used to test for the possible influence of the proportion of male associates amongst all the associates for male great tits on future divorce probability. These models were run as an additional check that intensiveness of competition for mates, rather than the absolute number of potential mates, influence the divorce probability. Other covariates include male between-sex degree, partner strength, and male's partner rank (i.e. how highly a male's breeding partner is on the list of all of his female 'friends') in the winter prior to the first breeding of a pair (i.e. winter in which a pair has formed) on the divorce probability of a pair to the next year. We controlled for winter (two levels: 2007 - 2009; and 2011), and the clutch size of a pair in each model. All models were run as binomial glm's in R.

Model structure (always including + clutch + winter)	AIC	Null deviance (df)	Residual deviance (df)
partner strength × m partner rank + m between sex degree + proportion of m associates	39.38	40.49 (35)	23.38 (28)
m partner rank + proportion of m associates	39.96	40.49 (35)	29.96 (31)
partner strength × m partner rank + proportion of m associates	41.16	40.49 (35)	27.16 (29)
partner strength × m partner rank + m between sex degree × m partner rank + proportion of m associates	41.19	40.49 (35)	23.19 (27)
partner strength × m partner rank + m partner rank × proportion of m associates	42.77	40.49 (35)	26.77 (28)
m between degree + proportion of m associates	43.01	40.49 (35)	33.01 (31)
partner strength + m between degree + proportion of m associates	43.25	40.49 (35)	31.25 (30)
m partner rank + m between degree + proportion of m associates	44.82	40.49 (35)	32.82 (30)
partner strength + m partner rank + proportion of m associates	44.90	40.49 (35)	32.90 (30)
proportion of m associates	45.89	40.49 (35)	37.89 (32)
partner strength + proportion of m associates	46.26	40.49 (35)	36.25 (31)
partner strength + m partner rank + m between degree + proportion of m associates	46.81	40.49 (35)	32.81 (29)

Table S2. 8 models (with support and the corresponding statistic for each) we used to test for the possible influence of the proportion of female associates amongst all the associates for female great tits on future divorce probability. These models were run as an additional check that intensiveness of competition for mates, rather than the absolute number of potential mates, influence the divorce probability. Other covariates include female between-sex degree, partner strength, and female's partner rank (i.e. how highly a female's breeding partner is on the list of all of her male 'friends') in the winter prior to the first breeding of a pair (i.e. winter in which a pair has formed) on the divorce probability of a pair to the next year. We controlled for winter (two levels: 2007 - 2009; and 2011), and the clutch size of a pair in each model. All models were run as binomial glm's in R. Compared to the corresponding model selection in males (Table S3), there were 4 models that (all containing the interaction between partner strength and female's partner rank) that were not possible to fit.

Model structure (always including + clutch + winter)	AIC	Null deviance (df)	Residual deviance (df)
partner strength + f partner rank + proportion of m associates	45.35	40.49 (35)	33.35 (30)
proportion of f associates	46.51	40.49 (35)	38.51 (32)
partner strength + proportion of f associates	46.68	40.49 (35)	36.68 (31)
partner strength + f partner rank + f between degree + proportion of f associates	46.95	40.49 (35)	32.95 (29)
f between degree + proportion of f associates	47.18	40.49 (35)	37.18 (31)
f partner rank + f between degree + proportion of m associates	47.65	40.49 (35)	35.65 (30)
f partner rank + proportion of f associates	47.71	40.49 (35)	37.71 (31)
partner strength + f between degree + proportion of f associates	48.30	40.49 (35)	36.30 (30)

Table S3. 6 models (with support and the corresponding statistic for each) testing the possible influence of females between-sex degree and her partner rank (i.e. position of her breeding partner on the list of all of her male ‘friends’) in the winter prior to the first breeding of a pair (i.e. winter in which a pair has formed) on the divorce probability of a pair to the next year. We controlled for winter (two levels: 2007 - 2009; and 2011), and the clutch size of a pair in each model. All models were run as binomial glm’s in R.

Model structure (always including + clutch + winter)	AIC	Null deviance (df)	Residual deviance (df)
-	44.57	40.49 (35)	38.57 (33)
partner strength	44.96	40.49 (35)	36.96 (32)
f between degree	45.29	40.49 (35)	37.29 (32)
partner strength + f partner rank + f between degree	45.42	40.49 (35)	33.42 (30)
f partner rank + f between degree	45.78	40.49 (35)	35.78 (31)
partner strength + f between degree	46.58	40.49 (35)	36.58 (31)

Table S4. Five models (with support and the corresponding statistic for each) testing the possible influence of male between-sex degree in the winter prior to the first breeding of a pair (i.e. winter in which a pair has formed) on the divorce probability of a pair to the next year. All males of newly formed pairs (irrespective of whether pair was or was not seen associated in winter) were included. We controlled for winter (two levels: 2007 - 2009; and 2011), and the clutch size of a pair in each model. The variable’ ever seen together’ can take value ‘yes’ if pair members were seen associate in winter, and value ‘no’ if they were not seen associated. All models were run as binomial glm’s in R.

Model structure (always including + clutch + winter)	AIC	Null deviance (df)	Residual deviance (df)
m between degree	53.53	50.92 (42)	45.53 (39)
m between degree + ever seen together	53.52	50.92 (42)	43.52 (38)
m between degree × ever seen together	53.87	50.92 (42)	41.87 (37)
-	56.84	50.92 (42)	50.84 (40)
ever seen together	57.90	50.92 (42)	57.90 (39)

Table S5. Five models (with support and the corresponding statistic for each) testing the possible influence of female between-sex degree in the winter prior to the first breeding of a pair (i.e. winter in which a pair has formed) on the divorce probability of a pair to the next year. All females of newly formed pairs (irrespective of whether pair was or was not seen associated in winter) were included. We controlled for winter (two levels: 2007-2009; and 2011), and the clutch size of a pair in each model. The variable' ever seen together' can take value 'yes' if pair members were seen associate in winter, and value 'no' if they were not seen associated. All models were run as binomial glm's in R.

Model structure (always including + clutch + winter)	AIC	Null deviance (df)	Residual deviance (df)
-	58.16	52.80 (45)	52.16 (43)
ever seen together	59.98	52.80 (45)	51.98 (42)
f between degree	59.71	52.80 (45)	51.71 (42)
f between degree + ever seen together	61.45	52.80 (45)	51.45 (41)
f between degree × ever seen together	62.75	52.80 (45)	50.75 (40)

CHAPTER 7

Benefits of familiarity: a selective advantage of early association in pair formation in great tits

Benefits of familiarity: a selective advantage of early association in pair formation in great tits

Antica Culina, Ben C. Sheldon, and Camilla A. Hinde

ABSTRACT

1. In socially monogamous birds the 'mate familiarity effect' has been suggested as one of the factors leading to greater breeding success across successive breeding attempts with the same partner.

2. Although the benefit of mate familiarity across successive breeding attempts has received some attention, the importance of the initial period of pair formation, before the first breeding, on breeding success has been largely unexplored. The period before breeding might not only influence breeding success, but also later pairing decisions, either directly, or indirectly through its effect on breeding success.

3. In this study we investigate the relationship between the length of the initial pairing period and 1) a pair's breeding success; and 2) its direct and indirect influence on the probability of a pair divorcing. To address these aims, we use 5 years of detailed data on winter social associations of individually marked great tits and breeding pairs in a wild population.

4. We show that early pair formation had a positive effect on laydate and fledging success (independently of laydate and clutch size), although the strength of the effect was different in different years. We did not detect any direct influence of the length of the initial pairing period on the future divorce probability. However, divorce probability could have been affected by the timing of pair formation indirectly, since it was correlated with clutch size and laydate.

5. By providing evidence that there is a selective advantage for a new pair to start associating earlier in winter, our study opens a new area in the study of the importance of pair bonding in socially monogamous birds. We call for more studies to explore the generality of our findings, and elucidate the mechanisms underlying the detected effects.

INTRODUCTION

In socially monogamous birds, repeated breeding with the same partner has been shown to bring fitness benefits through increased breeding success (Black 1996), and survival of pair members (Black 1996, Culina et al. 2013: Chapter 3). Both of these fitness benefits can be due to the ‘mate familiarity effect’ (Tinbergen 1959, Black 1996, Black 2001). Here, breeding success is thought to increase because of the improved coordination, cooperation and responsiveness between pair members (Weiss et al. 2010, Hirschenhauser 2012), while increased survival comes through shared vigilance and increased competitiveness (e.g. access to food or roosting sites) of a pair outside of the breeding season (Ekman 1990, Lemmon et al. 1997, Black 2001). In addition, the initial mate choice, prior to the first breeding with a partner, can be constrained by a lack of time, information, or cognitive constraints, and can therefore result in a formation of suboptimal partnerships. In this case secondary mating strategies, such as mating outside the social pair, divorcing the partner, or both, are often shown to increase the fitness of individuals (Petrie and Kempenaers 1998, Spottiswoode and Moller 2004, Bateson and Healy 2005).

Interestingly, most studies of the importance of mate familiarity have concentrated on the familiarity of pair members after they have bred together at least once, while the importance of associating with a partner before the first breeding of a pair has remained largely unexplored. A prolonged association with a future partner might be expected to increase breeding success through the mate familiarity effects (Griggio and Hoi 2011and references therein) and survival through nutritional benefits ('early pairing benefits', Rodway 2007). At the same time, the initial period of pair formation should influence mate choice decisions, as it can serve as a prolonged period of partner assessment (Rodway 2007, Leese 2012). Consequently, pairs with a longer initial period of pair formation should have more time to assess the partner and/or develop compatible behaviours that increase breeding success (see Spoon et al. 2006). These factors could be especially important in species with short life-spans where the first breeding attempt might also be the only attempt. However, only a few studies have acknowledged the topic so far (Bluhm 1988, Rodway 2007, Griggio and Hoi 2011, Hirschenhauser 2012), and only one (to our knowledge) has addressed it experimentally. In an experiment where bearded reedling (*Panurus biarmicus*) pairs were allowed to spend different amount of time together prior to their first breeding, Griggio and Hoi (2011) showed that the length of pair formation influenced breeding success. Pairs with a longer pair formation period were better synchronised in nest building behaviour, bred earlier, and had higher hatching and fledging success. The same effects should be expected in free-living populations, especially because of strong selection on earlier laydate through its influence on other components of breeding success (e.g. Svensson 1997, Sheldon et al. 2003, Ahola et al. 2012).

In this study our main aim was to test if there is a selective advantage of an early start of pair association for newly formed pairs in a free-living population of socially monogamous great tits (*Parus major*). Because early pairing could influence fledgling production both indirectly, through benefits associated with early laying, and indirectly by increased coordination of parental duties of familiar pairs (i.e. directly; see Fig 1), we tested how the length of pair formation affects different components of breeding success. Second, we tested whether pairs whose members started to associate earlier in the winter prior to the first breeding had a lower divorce probability the next breeding season. We expected to find this pattern because of the longer period of partner assessment (i.e. directly), and/or because of the second-order influences through breeding success (i.e. the indirect routes in Fig 1). In birds, pairs with lower breeding success divorce more often (Dubois and Cezilly 2002, Culina et al. 2014: Chapter 2), in which case later pair formation can indirectly lead to higher divorce probability through its influence on breeding success.

METHODS

Study species

The great tit is a small, short-lived, cavity-nesting passerine (Barnes 1975). In the UK, great tits are resident and spend the winter in mixed species flocks that are usually described as being relatively stable (however, this depends on the local ecological conditions, see Gosler 1993). Breeding pairs are generally formed between birds belonging to the same core winter flock (Hinde 1952, Bjorklund et al. 1989); it seems that new pairs mostly form after these flocks dissolve, with some pairs forming while still a part of the flock (Hinde 1952, Saitou 1979). Reported divorce rates in great tits are quite variable between populations, ranging between 0-51% (e.g. Dhondt et al. 1996).

Data collection and construction of social networks

Our data come from a wild population of great tits in Wytham Woods, Oxford (51° 46’ N, 1° 19’ W), where the majority of birds (estimated to be around 82% of all birds available to be tagged, Matechou et al. in press) are marked with passive integrated transporders (PIT-tags). We used data on social associations in winter flocks collected between the 2007 (i.e. 2007/2008 winter) and 2012 winters and data on breeding pairs collected between the 2008 and 2013 breeding seasons (i.e. in six breeding seasons preceded with winter observations). Data concerning winter flocks were collected using radio-frequency identifiacation (RFID) technology: PIT-tagged birds were detected on feeders equipped with antennae (Garroway et al. in press, Matechou et al. in press). During the winters of 2007, 2008, and 2009, data were collected between August and March, using a setup where 16 (of 67) feeders were open (and thus available for birds) at any time. Every four days open loggers were rotated around the 67 locations following a structured randomised design, so that each of 8 approximately equal-sized sections of the wood always had two active loggers in it. In the 2011 and 2012 winter a different design was used, with a total of 65 stationary feeders. In these winters feeders were open once a week, for two successive days, between early December and early March. In these ways the possibility that flocks would get attracted to the constant food sources was minimised, and we assume that data gathered at feeders represent a ‘snapshot’ of the social composition of a flock at the time of feeding. During the breeding season, identities of breeding pairs and their breeding success were collected using standardised protocols (Perrins 1965, Perrins 1979, Gosler 1993). Data on breeding success analysed here include laydate (date when the first egg was layed in the nest), clutch size (number of eggs in the nest), the number of hatched young (number of hatchlings in the nest), the number of fledged young (number of young that succesfully fledged from the nest), hatching success (proportion of eggs that hatched), and fledging success (proportion of hatchlings that fledged).

To determine when members of a pair started to associate we used the spatio-temporal detection of co-occurrence of individuals at loggers (i.e. gambit of the group approach, Franks et al. 2010). We applied the GMMEvent (Gaussian mixture model for event streams) method (Psorakis et al. 2012) to extract association matrices from the data collected on loggers. In the first three winters these matrices were constructed one for each month and for the 2011and 2012 winters one for each weekend of the data collection. We considered that the initial period of pair formation started in the month (in the first 3 winters) or the week (in the last 2 winters) when the members of the future breeding pair were first identified associating together. We considered only those pairs where individuals were tagged either prior to the winter of interest as nestlings or adults, or had been newly tagged as immigrants at least two sampling occasions before the first detection of a pair associating together. In this way we eliminated those cases where pair members might have been associating but not detected as associated because one or both members were not tagged at the time. In addition, we checked for the possibility that some tagged birds might have left the woods at the end of the breeding season, formed pairs outside of the main woods, and returned already paired. There were only 6 of cases (out of 388 pairs – i.e. <2%) where both birds were (i) known to be tagged prior to the winter, but (ii) detected for the first time in the late autumn/winter (i.e. after October) as already paired (i.e. after a gap in detection for both of the pair members). Finally, we want to emphasize that the time when a pair was detected together for the first time does not mean that a pair has actually formed yet. However, this is still relevant for the effects on the breeding success and divorce we looked at in this study, because the period between the first detection of the associating members and the breeding season represents time length they could have spent assessing each other and familiarising with each other.

Data analysis

To analyse the influence of the time when pair members started to associate on breeding success, and divorce probability to the next season, we considered only newly formed pairs. These pairs might be formed between birds that had already bred, but with a different partner to the one in the year of interest (we termed these birds 'old'), between two inexperienced birds (either first year breeders or immigrants, we termed these birds as 'new'), or a combination of the two. Consequently, we distinguished four types of pairs; both birds are old; both birds are new; female is old and male is new; male is old and female is new. We did so because breeding success may be influenced by the prior experience of both male and female (Harvey et al. 1979, Hatch and Westneat 2008), and the initial pairing period might have different implications for breeding success in different types of pairs. From breeding records, there were 172 pairs (with both members tagged) formed in the 2007, 2008 and 2009 winters. Amongst these, members of 32 pairs were never detected associating. There were 115 pairs formed in the 2011 winter and 101 pairs formed in the 2012 winter; of these 3, and 21, respectively, were not seen associated during winter logging. In all of these pairs one or both of the pair members were detected at feeders very rarly (i.e. in the lowest 20^{th} percentile of the distribution of the number of times each bird was detected in a given winter), or had a larger number of detections but in only one month/weekend. Moreover, there was no indication that breeding success at any stage was different between pairs detected and not detected associating (see Supplementary Table S1). Thus, we assumed that these pairs represented a mixed sample of all pairs, but were not detected associating because one or both members failed to be detected frequently. We continued our analysis with only those pairs where birds were detected associating.

As the protocol for data collection were different in the two periods of data collection (i.e. 2007 to 2009 winters; and 2011 and 2012 winters), we analysed these periods separately. We defined the date when pair members were first seen associated as a continuous variable. In winters 2007 to 2009 the value ranged between 1 (August) and 8 (March). In the 2011 winter the value ranged from 1 (week 1, Dec 2011) to 12 (week 3, Feb 2012; 12 weekends of data collection) and in the 2012 winter from 1 (week 1, Dec 2012) to 14 (week 1, March 2013).

When analysing the influence of time a pair was first recorded together on breeding success, our main response variables were: laydate (standardized per year), clutch size, number of chicks, number of fledglings, hatching success (proportion of eggs that hatched), and fledging success (proportion of hatchlings that fledged). Our main predictor variables were time of pair formation (continuous variable), type of a pair (categorical variable with 4 levels: both old; both new; female old and male new; male old and female new), and winter. Time of pair formation describes the length time since members of future breeding pairs first associated. After the initial data exploration (tree models, simple correlation coefficients), we applied generalised linear models (glm) containing possible variables that might influence breeding success (time of pair formation, type of a pair, winter). In addition, when there was an indication that the relationship was not linear, we applied non-linear models (GAMs) to the same data. In gam models, we applied a smoothing function to the term ‘time of pair formation’, either as one smoothing function (same for all winter and types of pairs), or as separate smoothing functions for each winter or type of a pair (this also included applying the smoothing function to some of winters/types of pairs). Because breeding success components were correlated (see Supplementary Table S2 for the correlation coefficients), we controlled for the preceding component of breeding success when modelling the influence of the time of pair formation on each component of breeding success; laydate was controlled when modelling the clutch size, clutch size for number of hatchlings, number of hatchlings for number of fledglings. We controlled for only laydate, and for both laydate and clutch size when exploring the influence of timing on pair formation on both hatching and fledging success. In this way we were able to separate direct and indirect effects of timing of pair formation on different components of breeding success. When modelling fledging success and the number of fledged young, we also repeated the analysis with only those pairs that had fledged at least one chick. In addition, we modelled a binary measure of fledging success (fledged at least one chick or not). We did this as complete fledging failure might happen due to an external cause, such as predation, and thus does not fully reflect parental ability to raise chicks. We did not apply the same procedure to hatching success and the number of hatchlings because all of the pairs (except two) in our analysis hatched at least one chick. In models with laydate as the response variable we used glm (and gam, where there was indication for the non-linear effects) models with Gaussian error distribution. In models with hatching success, or fledging success as the response variable we used glm (and gam) models with binomial error distribution. In models were the response variable was clutch size, number of hatchlings, or number of fledglings, we used glm (and gam) with the poisson error distribution. The basic list of model structures is given in the Table S3 (Supplement).

Next, we tested whether new pairs that began associating later in the winter before a given breeding season *t* divorced more often afterwards. This required that both members of a new pair were detected in winter, and that both had survived to breed in *t*+1 (either together – fidelity; or with new partners – divorce) leading to reduced sample sizes (Table 1). Consequently, we treated the first three winters (2007 to 2009) as one dataset. We did not include the data on pairs formed in the 2012 winter because we lacked the data on the 2014 breeding season (and thus were unable to score pairs as divorced or faithful).

Table 1. The number of pairs breeding together for the first time in the breeding season *t*, for which both partners were detected in the winter prior to *t*, and where both survived to the season *t*+1 to either breed together (fidelity) or with new partners (divorce). Status refers to the status in *t*+1 (divorced or faithful) of a pair that bred together in breeding season *t*. Winter refers to the winter prior to the breeding season *t*. For example, of 6 pairs that have formed in 2007 winter (and bred for the first time in 2008 breeding season), 3 divorced, and 3 remained faithful to the 2009 breeding season.

Status	Winter	2007	2008	2009	2011
Divorced		3	3	0	3
Faithful		3	9	3	12

Because time of pair formation might influence future divorce probability indirectly through low breeding success (Fig 1) we controlled for breeding success in the analysis. To decide on the component of breeding success to control for, we conducted a small meta-analysis on the correlation between breeding success and divorce probability using data on great tits and three closely related tit species (*Cyanistes caeruleus*, *Poecile montanus*, and *Poecile atricapillus*). The analysis included 10 papers with 63 effect sizes. We provide the details on the meta-analysis in the Supplement. The results of the meta-analysis have shown that the laydate and clutch size were the only components of breeding success that correlated with future divorce probability (correlation coefficient for laydate = 0.16, 95%CI = 0.07 - 0.24; for clutch size = 0.12, 95%CI = 0.04 - 0.20). Thus, we controlled for either clutch size or laydate in the models. We used glm with binomial error structure and status in *t*+1 as a binomial response (divorced or faithful). To keep the models simple (due to the small sample size) we only considered six possible structures for the explanatory part of the model: intercept model, ‘clutch size’, ‘clutch size + time of pair formation’, ‘laydate’, ‘laydate + time of pair formation’, ‘time of pair formation’.

All of the analyses were conducted in the R programming language. We compared models with different structures using the AIC values (Anderson and Burnham 2002). We considered that a model gained better support if its AIC value was 3 or more units lower than the AIC value of the competing model (models).

RESULTS

The time period when the majority of new pairs were first detected associating was different in different winters (Supplementary Fig S1). In the first three winters (i.e. 2007 to 2009) when data were collected monthly, there was a clear peak around September and October. However, later distribution was year-specific. In 2011 and 2012 winters, when data were collected weekly and the collection started only in December, the large majority of pairs were first time detected associated in the first weekend of data collection. This presumably means that they started to associate even earlier.

Pair association date and breeding success

The best supported models on the 2007 – 2009 dataset revealed that the timing of pair association influenced laydate and fledging success independently (see Supplementary Table S4 and S9 for details on model selection). The best supported model included time of pair formation and winter (Table 2). Laydate correlated with the time of pair formation in one out of three winters (in 2007 F-value = 2.74, df = 3.91, p-value = 0.032, for the smoothing term of the best model) in a non-linear fashion (Fig 2, Table 2).

Table 2. Best supported models testing for the influence of time of pair formation on laydate, and fledging success on the 2007 - 2009 winter (2008 - 2010 breeding season) dataset. Structure of the best laydate model: laydate ~ s (time of pair formation, by = winter 2007, k=8) + winter; with Gaussian error structure. Structure of the best fledging success model: time of pair formation x type of a pair + winter + laydate + clutch size; with binomial error structure and corrected for overspersion. Type of a pair: female new breeder and male old breeder ('NO'), female old and male new ('ON'), both new ('NN'), both old ('OO').

Dependant variable	Coefficients	Estimate	Std Error	t-value (F-value for the smoothed term)	p for the t-value (or F- value)
laydate	global intercept	0.172	0.191	0.902	0.369
	winter 2008	-0.277	0.204	-1.360	0.176
	winter 2009	-0.453	0.200	-2.267	0.025
	time of pair formation (only 2007 winter)	-	-	2.739	0.032
fledging success	global intercept	10.197	1.600	6.370	<0.001
	time of pair formation	-1.092	0.233	-4.681	<0.001
	2008	-0.061	0.514	-0.119	0.905
	2009	-0.997	0.599	-1.665	0.096
	'NO' pairs	-4.017	1.491	-2.692	0.007
	'ON' pairs	-5.202	1.392	-3.736	<0.001
	'OO' pairs	-6.414	1.412	-4.542	<0.001
	laydate	0.080	0.139	0.580	0.562
	clutch size	-0.214	0.059	-3.606	<0.001
	time of pair formation 2008	0.251	0.119	2.107	0.035
	time of pair formation 2009	0.206	0.125	1.643	0.100
	time of pair formation 'NO' pairs	0.565	0.231	2.444	0.014
	time of pair formation 'ON' pairs	0.682	0.209	3.257	0.001
	time of pair formation 'OO' pairs	0.884	0.224	3.940	<0.001

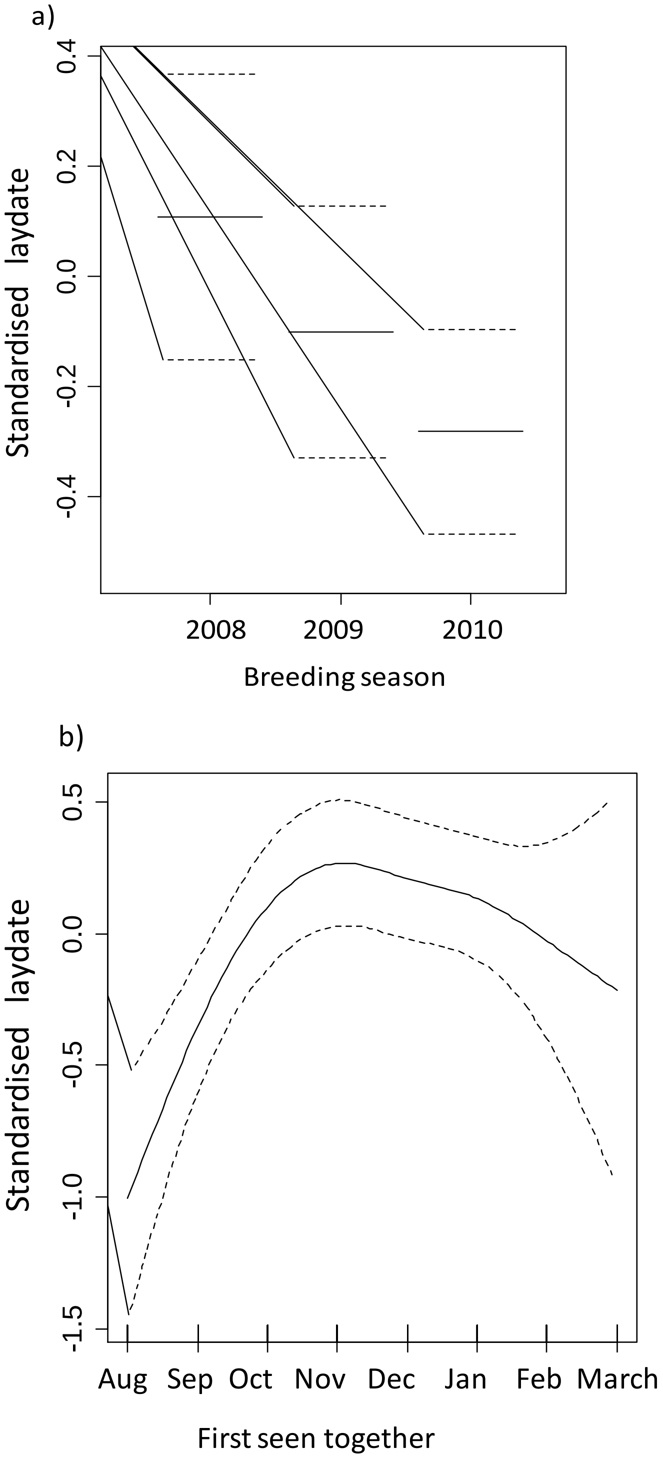


Figure 2. Standardised (for year and for all breeding pairs) laydate of newly formed pairs of great tits a) in 2008, 2009 and 2010 breeding seasons (mean and 2 SE); and b) in 2008 breeding season as a non-linear function of the time when a pair of breeding great tits was first seen together (August to March) in 2007 winter with the 2 SE standard errors of the estimate (dashed

lines); as obtained by the best additive model (laydate ~ s (time of pair formation, by = winter 2007, k=8) + winter; with Gaussian error structure).

Pairs that started to associate in August had the earliest standardised laydate (-0.83, 95% CI = -1.53/-0.12) with laydate getting later for pairs starting to associate up to November (0.43, 95% CI = -0.82/0.06). Laydate advanced slightly for pairs starting to associate after November (up to -0.04, 95% CI = -1.24/1.16 in March). The best supported model in the set of models testing for the factors influencing fledging success included winter, laydate, clutch size, type of a pair, time of pair formation, and the interaction between the last two (see Table S9 for model selection, Table 2 for model output). The effect of time formation thus acted on fledging success independently of laydate and clutch size. We found that fledging success was higher for pairs that started to associate earlier in winter. This relationship depended on winter (Fig 3a) and the type of a pair (Fig 3b). The average fledging success of pairs that started to associate in August was 0.85 (95%CI = 0.78/0.89) and of those formed in March 0.63 (95% CI = 0.53/0.72). We did not find support for any influence of time of pair formation on the number of eggs, number of chicks, hatching success, or number of fledglings (for the details on model selection see Supplementary Tables S5 to S8, S10). Each of these stages depended only on the preceding component of breeding success (i.e. clutch size on laydate, number of hatchlings on clutch size, number of fledglings on number of hatchlings, hatching success on laydate).

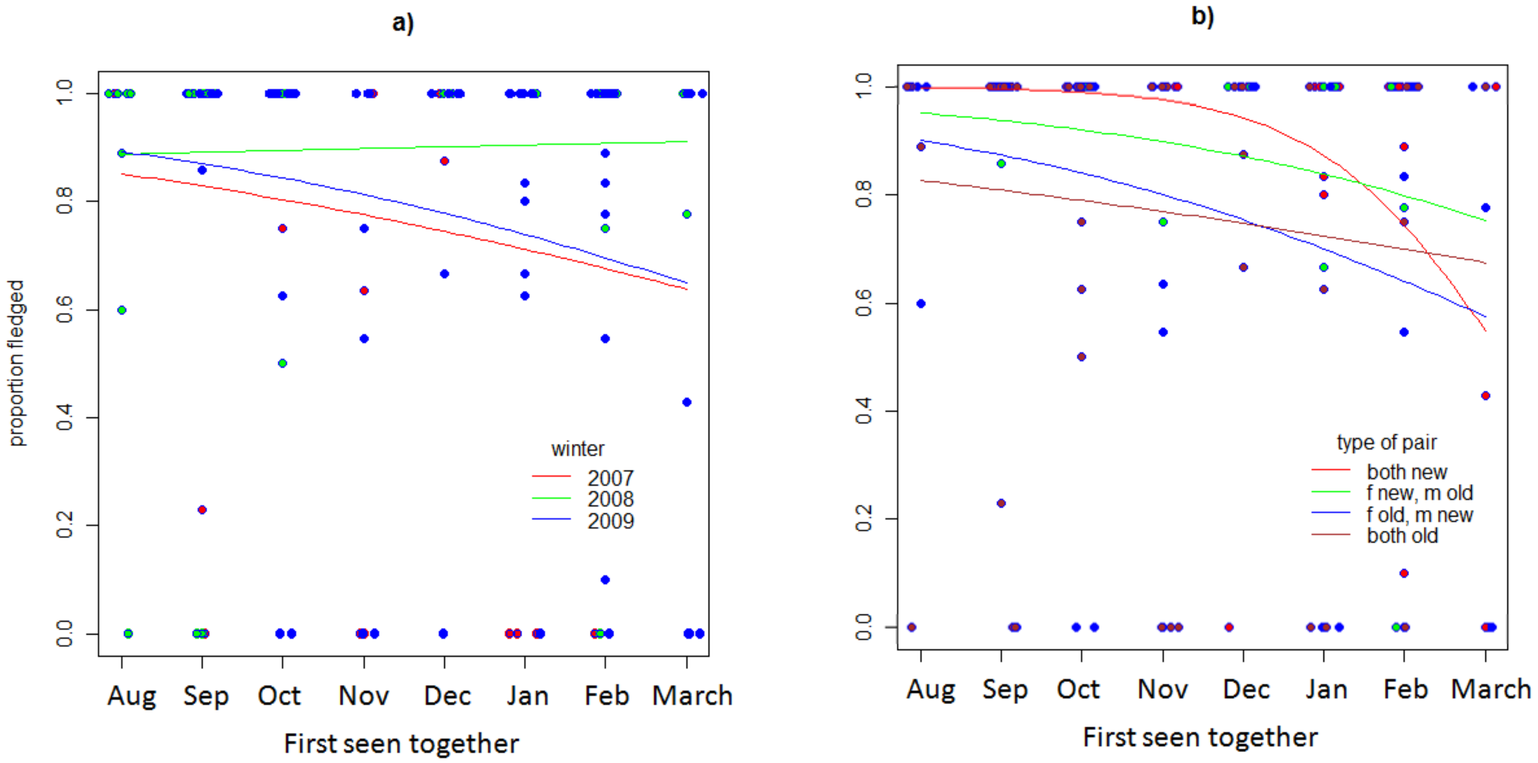


Figure 3. Correlation between fledging success and when a pair was first detected associating (August to March): a) in three different years (red = winter 2007; green = winter 2008; blue = winter 2009, and b) for four different types of pairs (red = both female and male are new breeders; green = female is a new breeder and male is an old breeder; blue = male is a new breeder, and femle is an old breeder; brown = both female and male are old breeders).

Model selection on the remaining two winters (2011 and 2012, Supplementary Table S11 to S17), revealed that time when a pair started to associate influenced laydate and fledging success. The best-supported laydate model included time of pair formation only (i.e. winter and the type of a pair were not selected for). The parameter estimate for the slope of time of pair formation was only 0.06 (SE = 0.02, p-value = 0.004), with laydate getting later with later start of pair-association (Fig 4). The best supported fledging success model included clutch size, laydate, winter, time of pair formation and pair type, and an interaction between the last two, and between winter and time of pair formation (Table S16). However, after accounting for over-dispersion, the term 'time of pair formation' lost statistical significance. Model selection on the factors influencing other components of breeding success did not suggest that any other component of breeding success was affected by the time of pair formation (Supplementary Tables S12-S15, S17).

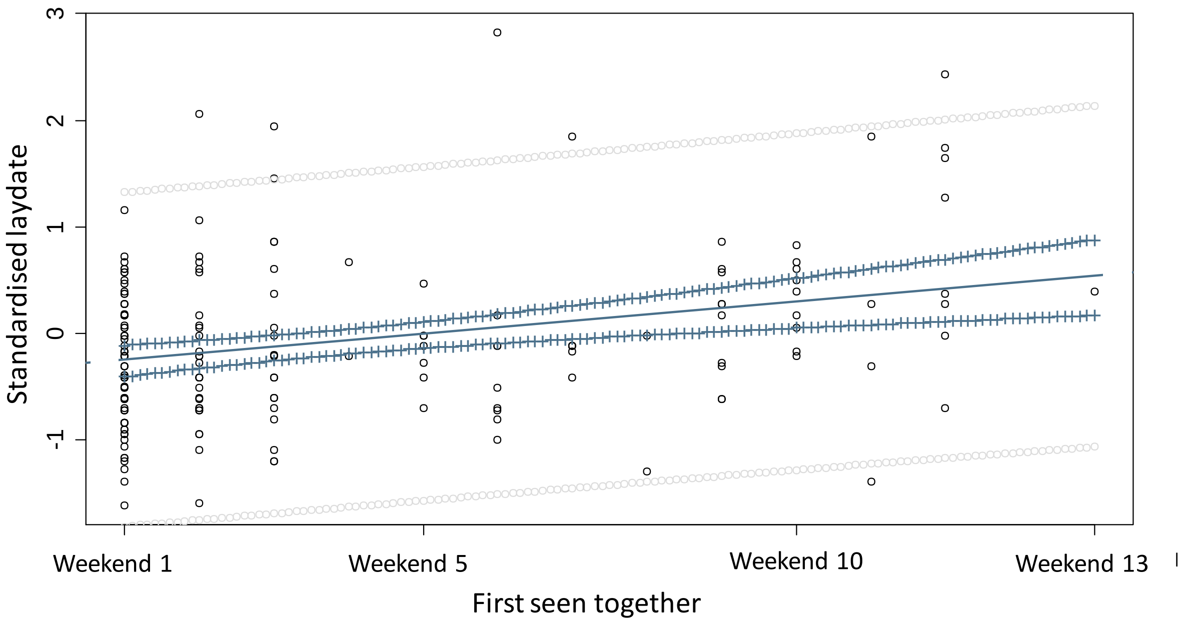


Figure 4. Estimated regressions line for the correlation between standardised laydate and winter weekend when pair was detected associating for the first time in winters 2011 and 2012. Grey circles represent the prediction intervals, and blue crosses the 95% confidence intervals for the regression line. Weekend when pair was first detected to associate ranges from 1 (weekend 3rd/4th Dec) to 12 (18th/19th Feb) in 2011, and 1 (1st/2nd Dec) to 14 (2nd/3d March) in 2012.

Time of pair formation and future divorce probability

Model selection on the influence of time of pair formation on future divorce probability for the combined 2007 to 2009 winters gave similar (and the best) support to two models (Supplementary Table S18). One included only ‘laydate’ as the main predictor of divorce of a pair, and the other one both ‘time of pair formation’ and ‘laydate’. Thus, there was no support that time of pair formation influenced divorce probability directly. Model selection on the 2011 winter returned three best-supported models. Models including time of pair formation (both controlling and not controlling for clutch size, or laydate, Supplementary Table S19) gained better support in the terms of AIC values than the models without it. However, the term ‘time of pair formation’ was not statistically significant in these models.

DISCUSSION

Our results show links between when pair members begin to associate and their subsequent success. Specifically, in some of the studied years, we found that earlier laydate and higher fledging success, correlated with longer initial pair formation period (i.e. earlier start of association between pair members). Moreover, the strength of the correlation was dependent on the year and the type of a pair (i.e. whether male and female are new or old breeders). On the other hand, our results did not support any direct influence of the initial pairing period on the future divorce probability (Fig 1). The benefits of early pair formation have primarily been addressed in long-lived species; in these species future pair members can start to associate several years prior to their first breeding (Rodway 2007, Hirschenhauser 2012). Three main functions have been suggested to explain these early pairings: direct benefits though higher winter survival of bonded individuals, benefits of within pair coordination leading to higher breeding success, and benefits of the prolonged period of partner assessment. Our study is, to our knowledge, the first to have detected direct breeding success benefits of early pair formation in a wild population of a small passerine bird.

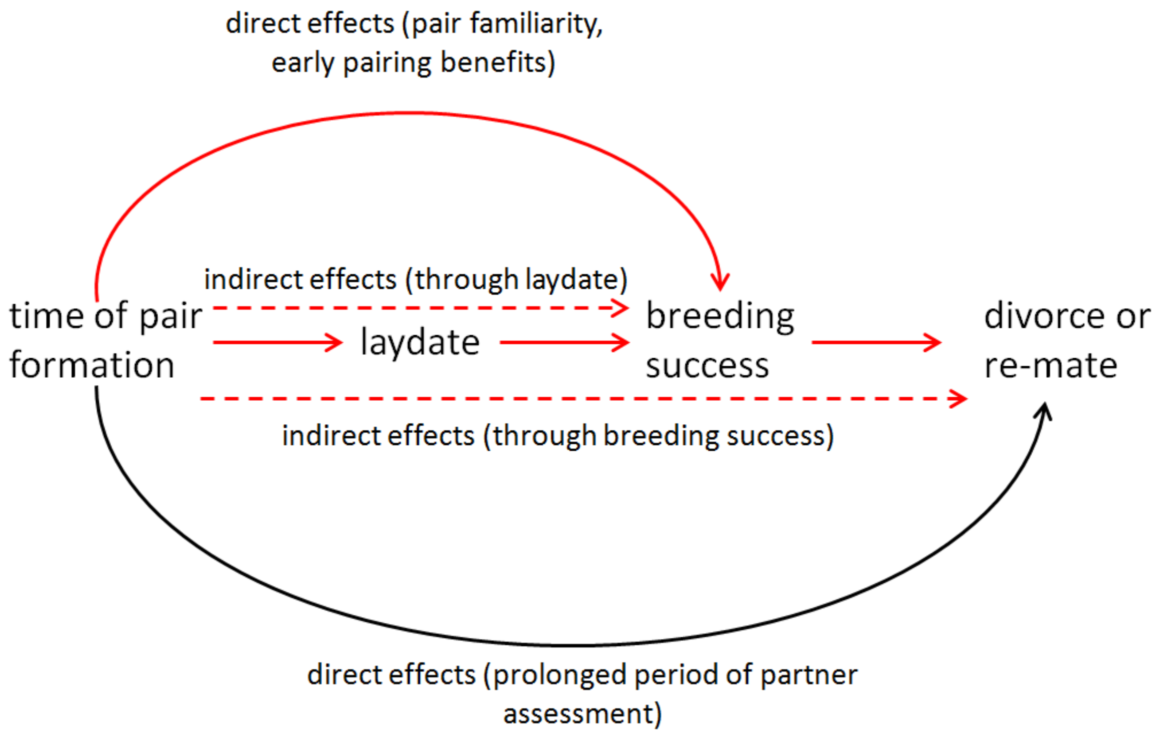


Figure 1. A schematic representation on the possible mechanisms (and the ones we detected to act in our great tit population, in red) through which time of pair formation can influence breeding success (i.e. components of breeding success other than laydate) and later mating decisions (i.e. breed with the same partner, or divorce a partner). If the influence is direct, this is represented by full arrows, and if it is indirect (i.e. acting through one or more other mediators) the arrows are dashed.

Strong selection for earlier laydate has been found in multiple great tit populations, including the population studied here (Perrins 1970, Verhulst et al. 1995, Garant et al. 2004, McCleery et al. 2004, Garant et al. 2007). Thus our finding that earlier pair formation can lead to earlier laydates implies that there might be a selective advantage of earlier pairing in a wild population of a small passerine bird and that the 'pair familiarity effects' can extend to familiarity of partners prior to their first breeding. There are different possible mechanisms through which an earlier start of association of pair members might influence the onset of breeding. For example, these pairs might be able to select better nest sites, and/or to synchronise their reproductive physiology better (Hirschenhauser 2012). We also detected that the correlation between the time when partners started to associate and their laydate is not evident in all years (three out of five years here). This is probably related to year-specific effects, which are at the same time reflected in the level of breeding-synchronisation of the population. If, for any reason, the majority of birds start to breed at roughly the same time, than the effect of the earlier pair formation is likely to disappear or be less strong. Our data support this possibility, because the 2008 breeding season had a much more evenly spread laydate, while in 2009 and 2010 there was a strong laying peak at the beginning of the season.

Moreover, the relationship between laydate in the 2008 breeding season and the time when a pair started to associate in the 2007 winter was not linear. Rather, between August and November pairs that started to associate earlier had an earlier laydate, but between November and March, birds that started to associate later had slightly enhanced laydate. This finding is partly in accordance with the finding from the captive bearded reedlings where pairs with the longest pairing period (i.e. 6.5 months) performed significantly better than pars with a short pairing period (i.e. on month), but there was no difference between short and medium (i.e. 4 months) pairing periods (Griggio and Hoi 2011). Moreover, our finding that the effect of the earlier association of pair members was less strong in the 2012 and 2013, when the data collection started only in December, is in accordance with the possibility that the benefits of earlier pairing are not very prominent after November. Another possibility is that the influx of new individuals, and the return of some birds that leave the woods during winter, but come back to breed (Matechou et al. in press), increases the pool of potential partners, and that these birds, for any reason, tend to start breeding earlier.

The second component of breeding success we found to be directly positively correlated with the length of the early pairing period was fledging success. While the other components of breeding success (i.e. clutch size, number of hatchlings and fledglings, hatching success) were only dependent on the previous components of success, fledging success was directly influenced by the length of the pairing period, even controlling for the laydate and clutch size (Fig 1&3). It has been suggested that cooperation and coordination between pair members of socially monogamous species is crucial for breeding success (Hirchenhauser 2013, Leese 2012 and references therein). If this coordination can be enhanced during the initial pairing period (as results of our study, and the study of Griggio and Hoi (2011) indicate), and the benefits of earlier pairing are different for birds of different experience (as suggested by our study), then the length of the initial pairing period might be interesting to study from the perspective of individual specific strategies of mate choice under the selective pressure for the earlier pair bonding. These are likely to depend on the range of factors, such as dominance, territory holding potential, inbreeding, and the availability of potential partners.

We found no evidence that the length of the initial pairing period influenced later divorce probability of a pair directly, but possibly through the breeding success of the pair (Fig 1). However, the models including time of pair formation were better supported than the models without this variable in the 2011 winter, although the timing of pair formation on later divorce probability in these models did not reach significance. This might indicate that the effect does exist, but that our data were too sparse to detect it.

Finally, we must acknowledge the possibility that birds of better quality, which also achieve higher reproductive success, pair earlier than birds of lower quality and that this causes the positive correlation between timing of pair formation and breeding success we detected in our study. We also want to emphasize that we did not consider short-term partnerships between males and females in our analysis. Some birds may begin to associate and then split up. More detailed data on association between sexes would be one way to better address the role of the initial pairing period for the assessment of the potential partners.

CONCLUSIONS

Our study shows, for the first time to our knowledge, that newly formed pairs appear to benefit from beginning to associate earlier in the winter, prior to the first breeding together, in a wild population of a short lived passerine bird. This was found in 3 out of 5 years studied. These benefits were mediated through direct effects on laydate and on fledging success. Although the underlying mechanisms are unknown, our study suggests that the benefits of pair familiarity in socially monogamous birds might not only be due to repeated breeding with the same partner, but also through a longer time of association prior to the first breeding of a pair. More studies including a range of different species, as well as experimental studies are needed to explore the generality of this pattern, and the mechanisms underlying it. Such studies would greatly increase our knowledge on the evolution and function of pair bonds and social monogamy.

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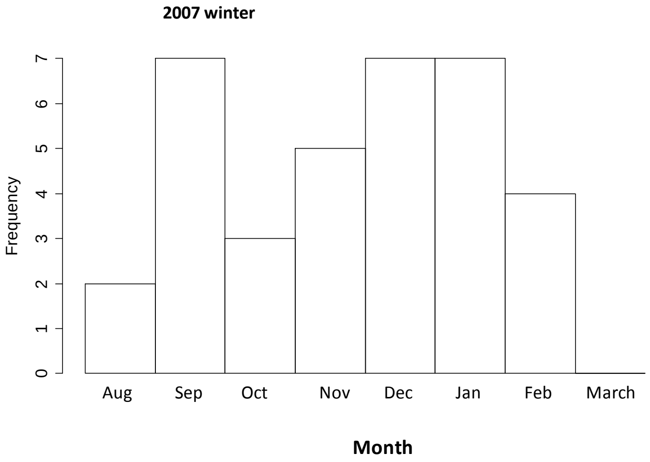
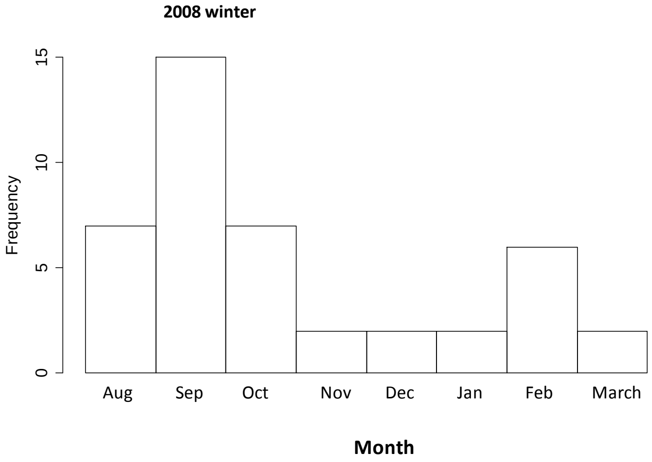
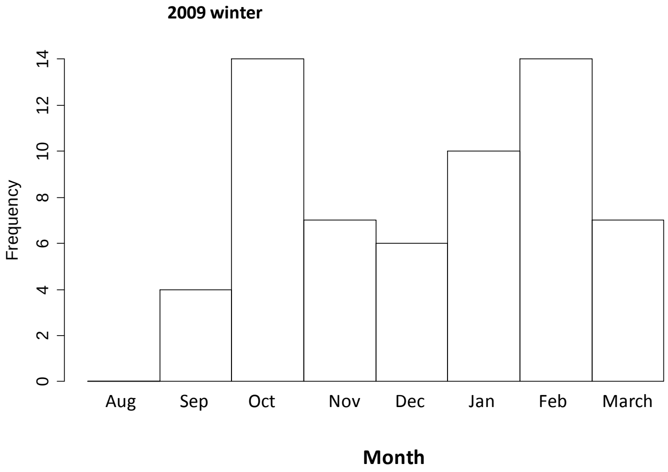
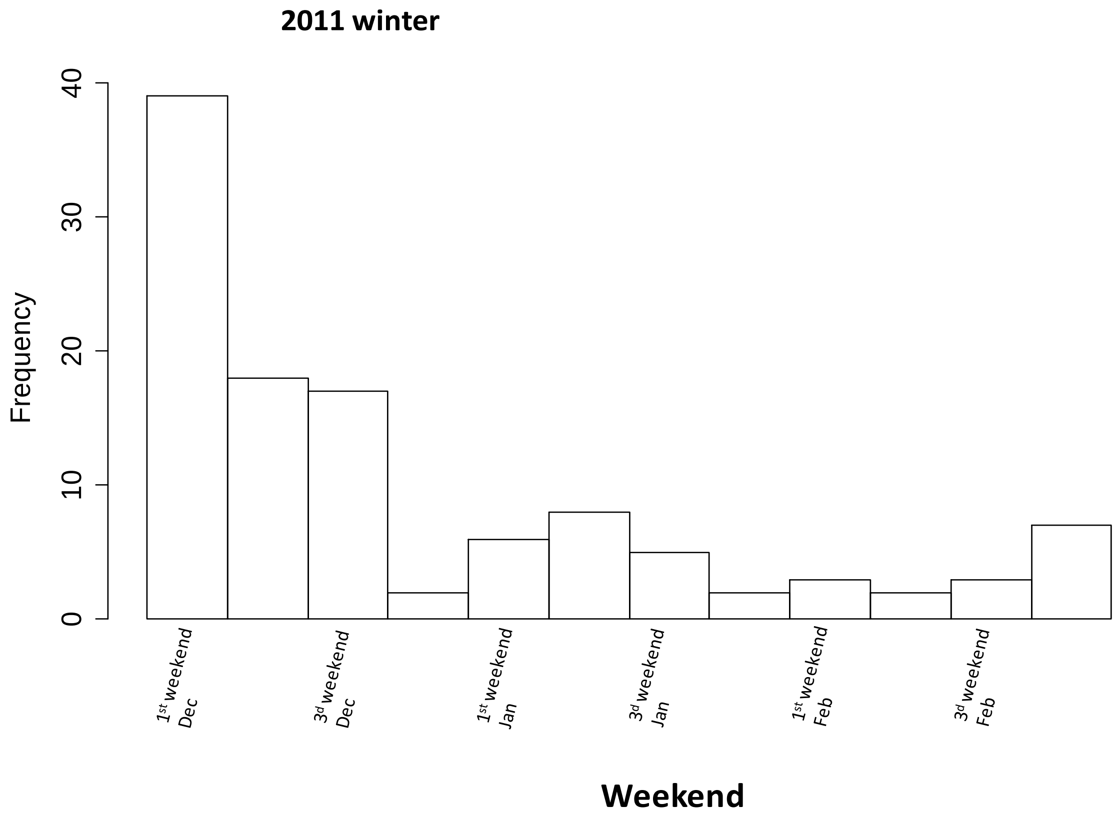
SUPPLEMENTARY FIGURES

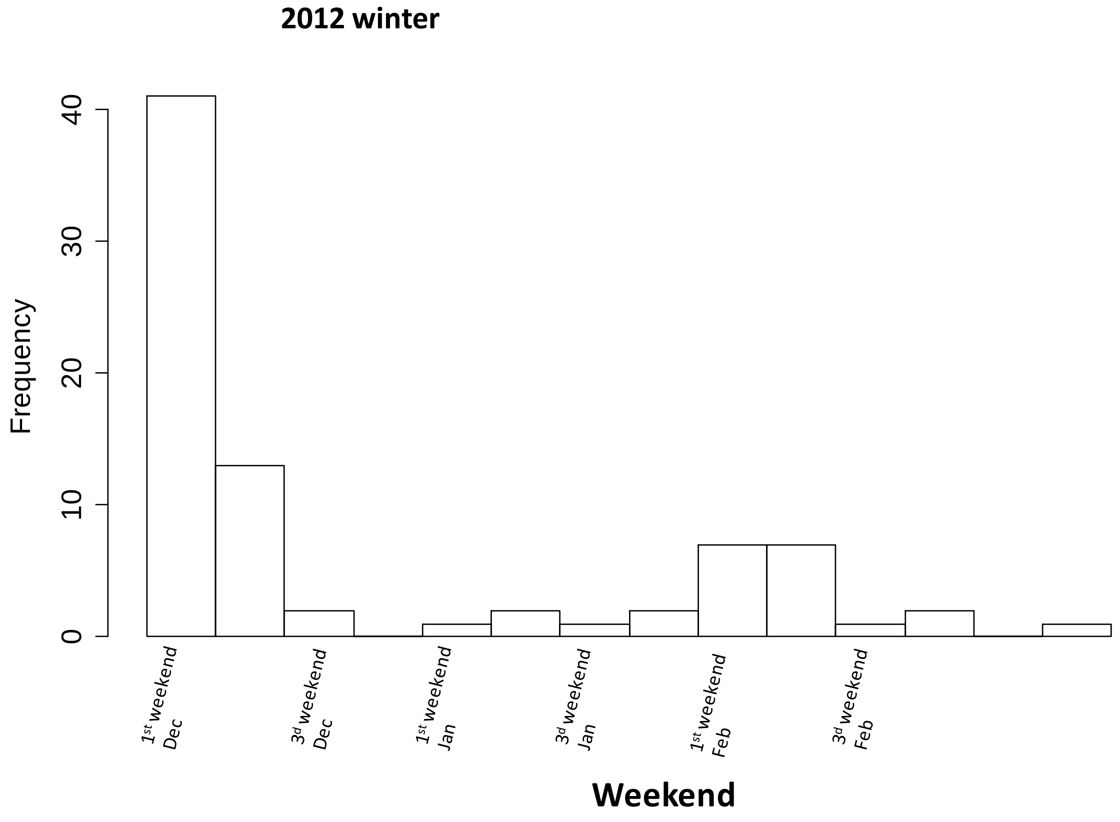
Figure S1. Histograms of the time when pair members of newly formed great tits pairs were first detected associating with each other. In the 2007 to 2009 winters these are different months (i.e. from Aug to March). In the 2011 and 2012 winters these are weekends: from 1st weekend in December (both winters) to last weekend of February (in 2011) and the second weekend of March (2012).








2011 winter


2012 winter

SUPPLEMENTARY TABLES

Table S1. Mean and standard deviation of the distribution of breeding success components for newly formed pairs of great tits in breeding seasons 2008 to 2010 (all years combined), and 2012 and 2013 (combined), according to whether a pair of birds (where each of the members was known to be tagged in the winter of interest, and each was seen at least at one sampling occasion) was or was not seen associating together in the winter prior to the breeding season. Breeding success is given as laydate (standardised for a year), clutch size, number of hatchlings, and number of fledglings. Test statistics for laydate is t-value from the two sample t-test, and for other components W statistics from the Wilcoxon rank sum test with continuity correction.

Breeding success component	Mean (sd)		Test statistics	p-value
	seen	not seen		
2008 to 2010				
laydate	-0.12 (0.69)	-0.12 (0.71)	-0.04	0.97
clutch size	9.19 (1.75)	8.94 (1.47)	2664.5	0.19
number of hatchlings	8.28 (2.17)	8.16 (1.83)	2467.5	0.36
number of fledglings	6.91 (3.43)	6.56 (3.28)	2462.0	0.38
2012 and 2013				
laydate	-0.11 (0.70)	-0.07 (0.65)	-0.16	0.87
clutch size	6.96 (1.46)	7.29 (1.58)	1980	0.25
number of hatchlings	6.12 (1.45)	6.06 (1.97)	2277	0.92
number of fledglings	5.00 (1.84)	4.43 (2.66)	2520	0.45

Table S2. Spearman rank correlation coefficients between different components of breeding success in breeding seasons 2008, 2009, 2010, 2012, and 2013. For fledging success (taking into account only those pairs that have fledged a chick) only correlation with laydate is provided as a Kendall's rank tau with the p-value. Correlation coefficients are given for all pairs and for those pairs that have fledged at least one chick (in brackets). Statistically significant (i.e. $p<0.05$) correlation coefficients are marked with an asterix.

Year	Component of breeding success	Clutch size	N of chicks	N of fledglings	Fledging success
2008	laydate	0.02 (0.04)	0.03 (0.11)	-0.17 (-0.10)	-0.23*
	clutch size	1	0.82* (0.85*)	0.38* (0.48*)	
	N of chicks	-	1	0.57* (0.62*)	
2009	laydate	-0.39* (-0.40*)	-0.54* (-0.51*)	-0.36* (0.38*)	0.18
	clutch size	1	0.75* (0.80*)	0.49* (0.72*)	
	N of chicks	-	1	0.71* (0.80*)	
2010	laydate	-0.36* (-0.33*)	-0.27* (-0.28*)	0.10 (-0.04)	0.21*
	clutch	1	0.74* (0.73*)	0.43* (0.55*)	
	N of chicks	-	1	0.63* (0.77*)	
2012	laydate	-0.21* (-0.24)	0.05 (0.01)	0.37* (0.36*)	0.33*
	clutch size	1	0.63* (0.65*)	0.36* (0.33*)	
	N of chicks	-	1	0.54* (0.62*)	
2013	laydate	-0.05 (-0.04)	-0.03 (-0.03)	0.20* (0.15)	0.23*
	clutch size	1	0.73* (0.76*)	0.50* (0.57*)	
	N of chicks	-	1	0.56* (0.68*)	

Table S3. Basic structure of 14 generalised linear models (glm), and generalised additive models (gam) contrasted to explore the influence of time of pair formation on breeding success: laydate (standardised per year), clutch size, number of hatchlings, number of fledglings, hatching success, and fledgling success. Error distribution used to model different components was Gaussian for laydate, Poisson for number of hatchlings and fledglings, and Binomial for hatching and fledging success. In models where the response was clutch size, number of hatchlings/fledglings, the preceding component of breeding success was added as an additive covariate to the model structure. In models where the response was hatching or fledgling success, laydate and laydate + clutch size, were added as an additive covariate to the model structure. In gam models, ‘s’ denotes that the smoothing function was fitted to the term, either as one smoothing function, or as separate smoothing function for each of the levels defined by ‘by=’. Our main predictor variables were time of pair formation (continuous variable), type of a pair (categorical variable with 4 categories: both old; both new; female old and male new; male old and female new), and winter. + = additive effect of a variable; × = interactive effect.

Type of model	Model structure (for the explanatory variables)
glm	time of pair formation × winter + time of pair formation × type of a pair + winter × type of a pair
	time of pair formation × winter + time of pair formation × type of a pair
	winter + time of pair formation × type of a pair
	winter + time of pair formation + type of a pair
	winter × time of pair formation + type of a pair
	time of pair formation + winter × type of a pair
	time of pair formation × winter
	time of pair formation × winter
	time of pair formation
	winter
	time of pair formation × type of a pair
	time of pair formation + type of a pair
	winter × type of a pair
	winter + type of a pair
gam	s(time of pair formation, k=8) + winter × type of a pair
	s(time of pair formation, k=8) + winter + type of a pair
	s(time of pair formation, k=8) + winter
	s(time of pair formation, by=winter, k=8) + winter
	s(time of pair formation, by=winter, k=8) + winter + type of a pair
	s(time of pair formation, by= type of a pair, k=8) + winter + type of a pair
	s(time of pair formation, k=8)
	winter
	time of pair formation

Table S4. Model selection on the factors influencing laydate (standardised per year) of newly formed great tit pairs in Wytham woods between 2007 and 2009 winters (2008 to 2010 breeding seasons). The overall best supported model is highlighted in bold.

Model structure, with Gaussian errors	AIC	df
Glm models		
winter	301.87	4
time of pair formation + winter	302.00	5
time of pair formation × winter	303.37	7
winter + type of a pair	306.33	7
winter + time of pair formation × type of a pair	306.95	11
time of pair formation	307.59	3
winter + time of pair formation + type of a pair	307.69	8
time of pair formation × winter + time of pair formation × type of a pair	308.40	13
winter × time of pair formation + type of a pair	308.98	10
type of a pair	311.19	5
time of pair formation + type of a pair	312.73	6
winter × type of a pair	313.31	13
time of pair formation × type of a pair	313.74	9
time of pair formation +winter × type of a pair	314.54	14
Gam models		
s(time of pair formation, by=winter 2007, k=8) + winter	**294.71**	**6.52**
s(time of pair formation, by=winter, k=8) + winter	298.70	8.50
winter	301.87	4.00
s(time of pair formation, k=8) + winter	301.46	5.56
s(time of pair formation, by=winter, k=8) + winter + type of a pair	304.50	11.47
s(time of pair formation, by= type of a pair, k=8) + winter + type of a pair	306.95	11.00
s(time of pair formation, k=8) + winter + type of a pair	307.07	8.58
s(time of pair formation, k=8)	307.14	3.50
time of pair formation	307.59	3.00
s(time of pair formation, k=8) + winter × type of a pair	314.19	14.4

Table S5. Model selection on the factors influencing clutch size of newly formed great tit pairs in Wytham woods between 2007 and 2009 winters (2008 to 2010 breeding seasons). Laydate is controlled in all of the models (i.e. + laydate).

Model structure, with Poisson errors	AIC	df
Glm models, all with + laydate		
time of pair formation	602.00	3
winter	603.75	4
type of a pair	605.06	5
time of pair formation + winter	605.29	5
time of pair formation + type of a pair	606.82	6
winter + type of a pair	608.47	7
time of pair formation × winter	608.76	7
time of pair formation + winter + type of a pair	610.22	8
time of pair formation × type of a pair	611.44	9
winter × time of pair formation + type of a pair	613.77	10
winter + time of pair formation × type of a pair	614.74	11
winter × type of a pair	617.89	13
time of pair formation × winter + time of pair formation × type of a pair	618.36	13
time of pair formation + winter × type of a pair	619.77	14
Gam models, all with + laydate		
s(time of pair formation, k=8)	602.00	3.00
winter	603.75	4.00
s(time of pair formation, k=8) + winter	605.29	5.00
s(time of pair formation, by=winter, k=8) + winter	608.76	7.00
s(time of pair formation, k=8) + winter + type of a pair	610.22	8.00
s(time of pair formation, by=winter, k=8) + winter + type of a pair	613.77	10.00
s(time of pair formation, by= type of a pair, k=8) + winter + type of a pair	614.74	11.00
s(time of pair formation, k=8) + winter × type of a pair	619.77	14.00

Table S6. Model selection on the factors influencing the number of hatched young of newly formed great tit pairs in Wytham woods between 2007 and 2009 winters (2008 to 2010 breeding seasons). Clutch size is controlled in all of the models (i.e. + clutch size).

Model structure, with Poisson errors	AIC	df
Glm models, all with + clutch size		
time of pair formation	602.00	3
winter	603.75	4
type of a pair	605.06	5
time of pair formation + winter	605.29	5
time of pair formation + type of a pair	606.82	6
winter + type of a pair	608.47	7
time of pair formation × winter	608.76	7
time of pair formation + winter + type of a pair	610.22	8
time of pair formation × type of a pair	611.44	9
winter × time of pair formation + type of a pair	613.77	10
winter + time of pair formation × type of a pair	614.74	11
winter × type of a pair	617.89	13
time of pair formation × winter + time of pair formation × type of a pair	618.36	14
time of pair formation + winter × type of a pair	619.77	13
Gam models, all with + clutch size		
s(time of pair formation, k=8)	602.00	3
winter	603.75	4
s(time of pair formation, k=8) + winter	605.29	5
s(time of pair formation, by=winter, k=8) + winter	608.76	7
s(time of pair formation, k=8) + winter + type of a pair	610.22	8
s(time of pair formation, by=winter, k=8) + winter + type of a pair	613.77	10
s(time of pair formation, by= type of a pair, k=8) + winter + type of a pair	614.74	11
s(time of pair formation, k=8) + winter × type of a pair	619.77	14

Table S7. Model selection on the factors influencing the number of fledged young of newly formed great tit pairs in Wytham woods between 2007 and 2009 winters (2008 to 2010 breeding seasons). Number of hatched young is controlled in all of the models (i.e. + number of hatched young). In the first set of models all pairs are included. In the second set of models only those pairs with at least one fledged young are included.

Model structure, with Poisson errors	AIC	df
Glm models, all with + n hatched		
time of pair formation	767.05	3
winter	767.65	4
time of pair formation + winter + type of a pair	768.06	8
time of pair formation + winter	768.08	5
time of pair formation + type of a pair	768.20	6
winter × time of pair formation + type of a pair	769.28	10
time of pair formation × winter	769.33	7
winter + type of a pair	770.11	7
winter + time of pair formation × type of a pair	770.84	11
time of pair formation × type of a pair	771.76	9
type of a pair	772.85	5
time of pair formation × winter + time of pair formation × type of a pair	773.43	13
time of pair formation + winter × type of a pair	777.16	14
winter × type of a pair	778.67	13
Glm models, all with + n hatched, only pairs that fledged >0 chicks		
time of pair formation	507.46	3
winter	508.81	4
time of pair formation + winter	510.58	5
type of a pair	512.05	5
time of pair formation + type of a pair	513.23	6
time of pair formation × winter	513.59	7
winter + type of a pair	514.62	7
time of pair formation + winter + type of a pair	516.18	8
time of pair formation × type of a pair	518.89	9
winter × time of pair formation + type of a pair	519.11	10
winter + time of pair formation × type of a pair	521.77	11
time of pair formation × winter + time of pair formation × type of a pair	525,06	13
winter × type of a pair	526.47	13
time of pair formation + winter × type of a pair	527.97	14

Table S8. Model selection on the factors influencing hatching success (i.e. proportion of eggs that hatched) of newly formed great tit pairs in Wytham woods between 2007 and 2009 winters (2008 to 2010 breeding seasons). First set of models are models where only laydate is controlled for, the second set the models where both laydate and clutch size are controlled for.

Model structure, with binomial errors	AIC	df
Glm models, all with + laydate		
winter + time of pair formation × type of a pair	378.12	11
time of pair formation × type of a pair	380.49	9
winter	381.12	4
time of pair formation × winter + time of pair formation × type of a pair	381.70	13
time of pair formation + winter	381.75	5
winter + type of a pair	382.03	7
winter + time of pair formation + type of a pair	383.76	8
time of pair formation	384.15	3
time of pair formation × winter	395.11	7
type of a pair	386.47	5
winter × type of a pair	386.85	13
winter × time of pair formation + type of a pair	387.35	10
time of pair formation +winter × type of a pair	388.58	14
time of pair formation + type of a pair	388.44	6
Glm models, all with + laydate + clutch size		
winter + time of pair formation × type of a pair	379.61	12
time of pair formation × type of a pair	382.18	10
winter	383.11	5
time of pair formation × winter + time of pair formation × type of a pair	383.25	14
time of pair formation + winter	383.69	6
winter + type of a pair	384.02	8
winter + time of pair formation + type of a pair	385.74	9
time of pair formation	386.15	4
time of pair formation × winter	387.08	8
type of a pair	388.47	6
winter × type of a pair	388.82	14
winter × time of pair formation + type of a pair	389.35	11
time of pair formation +winter × type of a pair	390.52	15
time of pair formation + type of a pair	390.43	7

Table S9. Model selection on the factors influencing fledging success (i.e. proportion of hatchlings that fledged) of newly formed great tit pairs in Wytham woods between 2007 and 2009 winters (2008 to 2010 breeding seasons). First set of models are models where only laydate is controlled for, the second set the models where both laydate and clutch size are controlled for, the third set of models where only those pairs with at least one fledged young are included.

Model structure, with binomial errors	AIC	df
Glm modles, all with + laydate		
time of pair formation × winter + time of pair formation × type of a pair	867.80	13
time of pair formation × winter + type of a pair	881.09	10
time of pair formation + winter × type of a pair	869.83	14
winter + time of pair formation × type of a pair	868.86	11
time of pair formation + winter + type of a pair	885.29	8
time of pair formation × winter	905.04	7
time of pair formation + winter	908.59	5
winter × type of a pair	892.04	13
winter + type of a pair	909.82	7
time of pair formation × type of a pair	892.39	9
time of pair formation + type of a pair	905.04	6
winter	920.45	4
time of pair formation	923.80	3
type of a pair	944.71	5
Glm models, all with + laydate + clutch size		
time of pair formation × winter + time of pair formation × type of a pair	856.57	14
time of pair formation × winter + type of a pair	870.34	11
time of pair formation + winter × type of a pair	858.37	15
winter + time of pair formation × type of a pair	857.43	12
time of pair formation + winter + type of a pair	872.67	9
time of pair formation × winter	894.16	8
time of pair formation + winter	894.80	6
winter × type of a pair	883.90	14
winter + type of a pair	901.19	8
time of pair formation × type of a pair	878.03	10
time of pair formation + type of a pair	889.87	7
winter	910.76	5
time of pair formation	908.55	4
type of a pair	935.66	6
Glm models, all with + laydate + clutch size, only pairs that fledged >0		
time of pair formation × winter + time of pair formation × type of a pair	295.59	14
time of pair formation × winter + type of a pair	296.02	11
time of pair formation + winter × type of a pair	305.25	15
winter + time of pair formation × type of a pair	298.70	12
time of pair formation + winter + type of a pair	304.61	9
time of pair formation × winter	301.88	8
time of pair formation + winter	306.75	6
winter × type of a pair	317.96	14
winter + type of a pair	314.39	8
time of pair formation × type of a pair	302.49	10
time of pair formation + type of a pair	307.78	7
winter	312.49	5

time of pair formation	308.97	4
type of a pair	324.57	6

Table S10. Model selection on the factors influencing binary fledging success (i.e. fledged at least one young vs. no young fledged) of newly formed great tit pairs in Wytham woods between 2007 and 2009 winters (2008 to 2010 breeding seasons). Laydate is controlled in all of the models (i.e. + laydate).

Model structure, with binomial errors	AIC	df
Glm modles, all with + laydate		
time of pair formation	122.72	3
winter	124.20	4
time of pair formation + type of a pair	124.98	6
time of pair formation + winter	125.42	5
winter + type of a pair	127.41	7
time of pair formation + winter + type of a pair	127.30	8
time of pair formation × winter	128.24	7
time of pair formation × type of a pair	129.08	9
time of pair formation × winter + type of a pair	130.18	10
winter + time of pair formation × type of a pair	131.11	11
winter × type of a pair	132.28	13
time of pair formation + winter × type of a pair	132.70	14

Table S11. Model selection on the factors influencing laydate (standardised per year) of newly formed great tit pairs in Wytham woods in 2011 and 2012 winters (2012 and 2013 breeding seasons).

Model structure, with Gaussian errors	AIC	df
Glm models		
time of pair formation	428.08	3
time of pair formation + winter	430.07	4
time of pair formation × winter	431.87	5
time of pair formation + type of a pair	433.30	6
time of pair formation × type of a pair	435.05	9
time of pair formation + winter + type of a pair	435.30	7
winter + time of pair formation × type of a pair	437.05	10
winter × time of pair formation + type of a pair	437.12	8
time of pair formation × winter + time of pair formation × type of a pair	438.80	11
time of pair formation + winter × type of a pair	440.27	10
winter	441.01	3
type of a pair	443.64	5
winter + type of a pair	445.65	6
winter × type of a pair	449.92	9

Table S12. Model selection on the factors influencing clutch size of newly formed great tit pairs in Wytham woods in 2011 and 2012 winters (2012 and 2013 breeding seasons). Laydate is controlled in all of the models (i.e. + laydate).

Model structure, with Poisson errors	AIC	df
Clutch size, all with + laydate		
winter	745.34	3
time of pair formation	745.61	3
time of pair formation + winter	746.14	4
time of pair formation × winter	747.99	5
type of a pair	748.85	5
time of pair formation + type of a pair	749.50	6
winter + type of a pair	749.79	6
time of pair formation + winter + type of a pair	750.47	7
winter × time of pair formation + type of a pair	752.35	8
time of pair formation × type of a pair	752.88	9
winter + time of pair formation × type of a pair	754.14	10
winter × type of a pair	755.32	9
time of pair formation × winter + time of pair formation × type of a pair	756.03	11
time of pair formation + winter × type of a pair	756.03	10

Table S13. Model selection on the factors influencing the number of hatched young of newly formed great tit pairs in Wytham woods in 2011 and 2012 winters (2012 and 2013 breeding seasons). Clutch size is controlled in all of the models (i.e. + clutch size).

Model structure, with Poisson errors	AIC	df
Glm models, all with + clutch size		
winter	779.40	3
time of pair formation + winter	779.86	4
time of pair formation	780.94	3
time of pair formation × winter	781.50	5
winter + type of a pair	784.58	6
time of pair formation + winter + type of a pair	785.10	7
type of a pair	785.30	5
time of pair formation + type of a pair	785.85	6
winter × time of pair formation + type of a pair	786.84	8
winter × type of a pair	789.14	9
time of pair formation + winter × type of a pair	789.92	10
winter + time of pair formation × type of a pair	790.19	10
time of pair formation × type of a pair	790.88	9
time of pair formation × winter + time of pair formation × type of a pair	792.12	11

Table S14. Model selection on the factors influencing the number of fledged young of newly formed great tit pairs in Wytham woods in 2011 and 2012 winters (2012 and 2012 breeding seasons). Number of hatched young is controlled in all of the models (i.e. + number of hatched young). In the first set of models all pairs are included. In the second set of models only those pairs with at least one fledged young are included.

Model structure, with Poisson errors	AIC	df
Glm models, all with + n hatched		
winter	886.72	3
time of pair formation × winter	887.89	5
time of pair formation + winter	888.72	4
winter + type of a pair	891.17	6
time of pair formation	891.74	3
winter × time of pair formation + type of a pair	892.43	8
type of a pair	893.00	5
time of pair formation + winter + type of a pair	893.17	7
time of pair formation × winter + time of pair formation × type of a pair	896.81	11
time of pair formation + winter × type of a pair	897.70	10
winter + time of pair formation × type of a pair	898.22	10
time of pair formation × type of a pair	900.16	9
time of pair formation + type of a pair	894.99	6
winter × type of a pair	895.73	9
Glm models, all with + n hatched, only pairs that fledged >0		
winter	621.25	3
time of pair formation	621.27	3
time of pair formation + winter	623.25	4
type of a pair	624.15	5
time of pair formation × winter	624.51	5
time of pair formation + type of a pair	626.11	6
winter + type of a pair	626.15	6
time of pair formation + winter + type of a pair	628.10	7
winter × time of pair formation + type of a pair	629.36	8
winter × type of a pair	630.90	9
time of pair formation × type of a pair	631.38	9
winter + time of pair formation × type of a pair	632.85	10
time of pair formation × winter + time of pair formation × type of a pair	633.97	11
time of pair formation + winter × type of a pair	633.27	10

Table S15. Model selection on the factors influencing hatching success (i.e. proportion of eggs that hatched) of newly formed great tit pairs in Wytham woods in 2011 and 2012 winters (2012 and 2013 breeding seasons). First set of models are models where only laydate are controlled for, and the second set the models where both laydate and clutch size are controlled for.

Model structure, with binomial errors	AIC	df
Glm models, all with + laydate		
winter + time of pair formation × type of a pair	601.59	10
time of pair formation + winter × type of a pair	603.51	10
time of pair formation × winter + time of pair formation × type of a pair	603.59	11
time of pair formation + winter + type of a pair	604.68	7
time of pair formation + winter	604.74	4
winter × type of a pair	604.82	9
time of pair formation × winter	605.74	5
winter × time of pair formation + type of a pair	606.58	8
winter	606.92	3
winter + type of a pair	607.11	6
time of pair formation × type of a pair	608.90	9
time of pair formation + type of a pair	613.15	6
time of pair formation	614.10	3
type of a pair	615.87	5
Glm models, all with + laydate + clutch size		
winter + time of pair formation × type of a pair	384.04	11
time of pair formation + winter	385.03	5
time of pair formation × type of a pair	385.29	10
time of pair formation × winter + time of pair formation × type of a pair	385.98	12
time of pair formation × winter	386.80	6
winter	386.83	4
time of pair formation + winter + type of a pair	388.00	8
time of pair formation	388.39	4
winter + type of a pair	389.65	7
time of pair formation + type of a pair	389.83	7
winter × time of pair formation + type of a pair	389.85	9
type of a pair	391.38	6
time of pair formation + winter × type of a pair	392.18	11
winter × type of a pair	393.36	10

Table S16. Model selection on the factors influencing fledging success (i.e. proportion of hatchlings that fledged) of newly formed great tit pairs in Wytham woods in 2011 and 2012 winters (2012 and 2013 breeding seasons). First set of models are models where only laydate is controlled for, the second set the models where both laydate and clutch size are controlled for, the third set of models where only those pairs with at least one fledged young are included.

Model structure, with binomial errors	AIC	df
Glm models, all with + laydate		
time of pair formation × winter + time of pair formation × type of a pair	880.81	11
time of pair formation × winter	884.98	5
winter × time of pair formation + type of a pair	887.33	8
winter + time of pair formation × type of a pair	891.14	10
winter	891.47	3
time of pair formation + winter	891.56	4
winter × type of a pair	892.35	9
winter + type of a pair	892.80	6
time of pair formation + winter × type of a pair	893.39	10
time of pair formation + winter + type of a pair	893.47	7
time of pair formation × type of a pair	899.44	9
type of a pair	900.29	5
time of pair formation + type of a pair	901.04	6
time of pair formation	902.31	3
Glm models, all with + laydate + clutch size		
time of pair formation × winter + time of pair formation × type of a pair	881.68	12
time of pair formation × winter	885.99	6
winter × time of pair formation + type of a pair	887.79	9
winter + time of pair formation × type of a pair	891.76	11
winter	892.34	4
time of pair formation + winter	892.48	5
winter × type of a pair	892.51	10
winter + type of a pair	893.05	7
time of pair formation + winter × type of a pair	893.63	11
time of pair formation + winter + type of a pair	893.79	8
time of pair formation × type of a pair	900.18	10
type of a pair	900.79	6
time of pair formation + type of a pair	901.61	7
time of pair formation	903.55	4
Glm models, all with + laydate + clutch size, only pairs that fledged >0		
time of pair formation × winter + time of pair formation × type of a pair	389.12	12
time of pair formation × type of a pair	389.97	10
winter + time of pair formation × type of a pair	391.17	11
winter × type of a pair	393.58	10
type of a pair	394.66	6
winter × time of pair formation + type of a pair	395.19	9
time of pair formation + winter × type of a pair	395.14	11
time of pair formation + type of a pair	395.69	7
winter + type of a pair	396.39	7
time of pair formation + winter + type of a pair	397.43	8
time of pair formation × winter	399.13	6
time of pair formation	399.50	4

winter	401.12	4
time of pair formation + winter	401.47	5

Table S17. Model selection on the factors influencing binary fledging success (i.e. fledged at least one young vs. no young fledged) of newly formed great tit pairs in Wytham woods in 2011 and 2012 winters (2012 and 2013 breeding seasons). Laydate is controlled in all of the models (i.e. + laydate).

Model structure, with binomial errors	AIC	df
Glm models, all with + laydate		
winter	155.01	3
time of pair formation + winter	156.42	4
time of pair formation × winter	157.15	5
winter + type of a pair	160.68	6
time of pair formation	160.78	3
winter × time of pair formation + type of a pair	162.62	8
time of pair formation + winter + type of a pair	162.01	7
winter + time of pair formation × type of a pair	163.06	10
time of pair formation × winter + time of pair formation × type of a pair	163.06	11
type of a pair	164.94	5
time of pair formation + type of a pair	166.48	6
winter × type of a pair	166.48	9
time of pair formation + winter × type of a pair	167.81	10
time of pair formation × type of a pair	169.32	9

Table S18. Model selection on the divorce probability of a pair between the breeding seasons *t* and *t*+1, in relation to time of pair formation in the winter preceding the breeding season *t*, and clutch size or the laydate of a pair in *t* for winters 2007 to 2009. All the models are glm's with a binomial error structure.

Model structure, with binomial errors	DIC	df
laydate	17.41	2
time of pair formation + laydate	18.31	3
time of pair formation	22.72	2
time of pair formation + clutch size	23.60	3
clutch size	27.63	2
intercept only	27.13	1

Table S19. Model selection on the divorce probability of a pair between the breeding seasons *t* and *t*+1, in relation to time of pair formation in the winter preceding the breeding season *t*, and clutch size or laydate of a pair in t for the 2011 winter. All the models are glm's with a binomial error structure.

Model structure, with binomial errors	DIC	df
time of pair formation	23.99	2
time of pair formation + clutch size	25.78	3
time of pair formation + laydate	25.99	3
intercept only	34.05	1
clutch size	34.48	2
laydate	34.66	2

SUPPLEMENTARY INFORMATION

Meta – analysis on the correlation between breeding success before divorce and divorce

We conducted a meta-analysis on the correlation between breeding success before divorce and divorce to decide on the component of breeding success (i.e. breeding stage) that has the strongest influence on divorce probability. We used a subset of data on Paridae species originally used in Culina et. al 2014 (*Parus major, Cyanistes caeruleus*, *Poecile montanus*, and *Poecile atricapillus*). The analysis included 10 papers with 63 effect sizes (Table S20). We used the 'MCMCglmm' package in R (Hadfield 2010) to conduct the analysis. We based model selection on the deviance information criterion (DIC), which is a Bayesian analogue of Akaike information criterion (AIC, Spiegelhalter et al. 2002). We considered a model that had the DIC value more than 4 units lower to be a better fit to the data than the competing model (or models). In addition, for each set of models, we also checked the significance of the fixed effects included in the models (using *P*-values provided in the MCMCglmm as pMCMC). We contrasted 6 different models (Table S21) in order to test whether models including stage of breeding influences the effect size. Our response variable was Fishers-Z score (normal transformation of Pearson's correlation coefficient r), and our predictor variables were: stage of breeding cycle (this can be: timing of breeding, clutch size, brood level measures, and fledgling level measures); dichotomisation of breeding success (whether or not breeding success was dichotomised); reference pairing class (i.e. whether breeding success of divorced birds was compared to faithful birds, widowed birds, or population mean). We also included 'population' as the random effect. Population corresponded to the study (i.e. main paper) in all but one case (Dhondt et al. 1996) where two populations were included in one paper. Each analysis was run for 5,000,000 iterations, burn-in of 500,000, and thinning interval of 10. Two models gained similar (and the best support) in the set of models tested: one that included 'breeding stage' + 'reference pairing class'; and the other one 'breeding stage' + 'dichotomisation' + 'reference pairing class (TableS2).

Table S20 Data on the correlation between breeding success and divorce used to perform the meta-analysis to detect which component of breeding success is a strongest predictor to divorce in four Paridae species (*Parus major*, *Cyanistes caeruleus*, *Poecile montanus*, and *Poecile atricapillus*).

Latine name	Population	Sample size	Breeding stage	Dichotomisation	Reference pairing class	Pearson's r	Fisher's-Z	error
Poecile atricapillus	Ramsay et al., 2000	26	fledging	yes	faithful	-0.13	-0.14	0.21
Poecile atricapillus	Ramsay et al., 2000	25	clutch	no	faithful	0.10	0.10	0.21
Cyanistes caeruleus	Ramsay et al., 2000	137	timing	no	faithful	0.11	0.11	0.09
Cyanistes caeruleus	Ramsay et al., 2000	137	clutch	no	faithful	0.07	0.07	0.09
Cyanistes caeruleus	Ramsay et al., 2000	137	fledging	no	faithful	0.02	0.02	0.09
Cyanistes caeruleus	Dhondt and Adriaensen, 1994	147	clutch	no	faithful	0.23	0.24	0.08
Cyanistes caeruleus	Dhondt and Adriaensen, 1994	147	fledging	no	faithful	0.24	0.25	0.08
Cyanistes caeruleus	Dhondt and Adriaensen, 1994	147	timing	no	faithful	0.34	0.35	0.08
Cyanistes caeruleus	Garcia-Navas and Sanz, 2011	42	clutch	no	faithful	0.17	0.17	0.16
Cyanistes caeruleus	Garcia-Navas and Sanz, 2011	42	brood	no	faithful	0.11	0.11	0.16
Cyanistes caeruleus	Garcia-Navas and Sanz, 2011	42	fledging	no	faithful	0.02	0.02	0.16
Cyanistes caeruleus	Kempenaers et al., 1998	35	brood	no	faithful	-0.29	-0.30	0.18

Cyanistes caeruleus	Pampus et al., 2005	90	brood	no	faithful	-0.18	-0.18	0.11
Cyanistes caeruleus	Pampus et al., 2005	90	brood	no	faithful	-0.08	-0.08	0.11
Cyanistes caeruleus	Pampus et al., 2005	90	clutch	no	faithful	0.04	0.04	0.11
Cyanistes caeruleus	Pampus et al., 2005	90	fledging	no	faithful	0.03	0.03	0.11
Cyanistes caeruleus	Pampus et al., 2005	90	fledging	no	faithful	-0.07	-0.07	0.11
Cyanistes caeruleus	Valcu and Kempenaers, 2008	38	fledging	no	faithful	-0.01	-0.01	0.17
Cyanistes caeruleus	Valcu and Kempenaers, 2008	38	fledging	no	faithful	0.18	0.18	0.17
Cyanistes caeruleus	Valcu and Kempenaers, 2008	38	clutch	no	faithful	0.34	0.35	0.17
Cyanistes caeruleus	Valcu and Kempenaers, 2008	38	clutch	no	faithful	0.37	0.38	0.17
Cyanistes caeruleus	Valcu and Kempenaers, 2008	38	timing	no	faithful	-0.65	-0.78	0.17
Cyanistes caeruleus	Blondel et al., 2000	81	clutch	no	population mean	0.03	0.03	0.11
Cyanistes caeruleus	Blondel et al., 2000	81	timing	no	population mean	0.19	0.20	0.11
Cyanistes caeruleus	Blondel et al., 2000	81	fledging	no	population mean	-0.37	-0.39	0.11
Cyanistes caeruleus	Blondel et al., 2000	81	fledging	no	population mean	-0.35	-0.37	0.11
Cyanistes caeruleus	Dhondt and Adriaensen, 1994	61	timing	no	population mean	0.00	0.00	0.13
Parus major	Dhondt et al. 1996, population 1	57	clutch	no	faithful	0.08	0.08	0.14
Parus major	Dhondt et al. 1996, population 2	57	fledging	no	faithful	0.05	0.05	0.14
Parus major	Dhondt et al. 1996, population 2	57	timing	no	faithful	0.04	0.04	0.14
Parus major	Kempenaers et al., 1998	83	brood	yes	faithful	-0.11	-0.11	0.11
Parus major	Pampus et al., 2005	50	fledging	no	faithful	0.31	0.32	0.15

Parus major	Pampus et al., 2005	51	brood	no	faithful	-0.21	-0.21	0.14
Parus major	Pampus et al., 2005	50	clutch	no	faithful	-0.18	-0.18	0.15
Parus major	Pampus et al., 2005	50	brood	no	faithful	-0.11	-0.11	0.15
Parus major	Pampus et al., 2005	51	fledging	no	faithful	0.23	0.23	0.14
Parus major	Pampus et al., 2005	50	fledging	no	faithful	-0.03	-0.03	0.15
Parus major	Pampus et al., 2005	50	brood	no	faithful	-0.18	-0.18	0.15
Parus major	Pampus et al., 2005	51	clutch	no	faithful	0.19	0.19	0.14
Parus major	Pampus et al., 2005	51	brood	no	faithful	-0.04	-0.04	0.14
Parus major	Pampus et al., 2005	50	fledging	no	faithful	0.10	0.10	0.15
Parus major	Saitou, 2001	287	clutch	no	faithful	0.07	0.07	0.06
Parus major	Saitou, 2001	287	fledging	no	faithful	0.12	0.12	0.06
Parus major	Saitou, 2001	287	timing	no	faithful	0.00	0.00	0.06
Poecile montanus	Orell et al., 1994	223	fledging	yes	faithful	0.03	0.03	0.07
Poecile montanus	Orell et al., 1994	92	fledging	no	faithful	0.05	0.05	0.11
Poecile montanus	Orell et al., 1994	92	fledging	no	faithful	0.06	0.06	0.11
Poecile montanus	Orell et al., 1994	121	clutch	no	faithful	0.10	0.10	0.09
Poecile montanus	Orell et al., 1994	117	clutch	no	faithful	0.16	0.16	0.09
Poecile montanus	Orell et al., 1994	129	timing	no	faithful	0.22	0.22	0.09
Poecile montanus	Orell et al., 1994	127	timing	no	faithful	0.24	0.24	0.09
Poecile montanus	Orell et al., 1994	223	timing	no	faithful	0.25	0.26	0.07

Poecile montanus	Orell et al., 1994	223	timing	no	faithful	0.18	0.18	0.07
Poecile montanus	Orell et al., 1994	215	clutch	no	faithful	0.15	0.15	0.07
Poecile montanus	Orell et al., 1994	203	brood	no	faithful	0.11	0.11	0.07
Poecile montanus	Orell et al., 1994	189	fledging	no	faithful	0.04	0.04	0.07
Poecile montanus	Orell et al., 1994	66	fledging	no	widowed	-0.02	-0.02	0.13
Poecile montanus	Orell et al., 1994	89	clutch	no	widowed	0.07	0.07	0.11
Poecile montanus	Orell et al., 1994	82	clutch	no	widowed	0.13	0.14	0.11
Poecile montanus	Orell et al., 1994	64	fledging	no	widowed	-0.15	-0.15	0.13
Poecile montanus	Orell et al., 1994	93	timing	no	widowed	0.24	0.25	0.11
Poecile montanus	Orell et al., 1994	90	timing	no	widowed	0.33	0.34	0.11

Table S21. Model summary of MCMC modelling of the effect size of the relationship between breeding success before divorce and divorce. All models have the same random-effect structure including the 'population' studied. Breeding stage represents the stage of breeding cycle.

Fixed-effect structure of the model	DIC	Delta DIC
breeding stage + reference pairing class	-120.27	0
breeding stage + dichotomisation + reference pairing class	-117.56	2.27
breeding stage	-98.45	21.82
dichotomisation + reference pairing class	-95.32	24.95
reference pairing class	-91.84	28.43
intercept only	-75.03	45.24

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CHAPTER 8

General discussion

General discussion

Aims and motivation

The primary aim of this work was to increase current understanding of pair bond dynamics in socially monogamous birds. The seminal book ‘Partnerships in Birds: Study of Monogamy’ (Black 1996) made two significant steps in the area. First, it emphasised the importance of continuous (i.e. life-long) processes of mate choice that can be expressed through extra-pair matings and through re-mating strategies (i.e. whether to re-mate with the same partner or to divorce it). Second, Black pointed out that the functional significance of a pair bond is not only (as previously considered) to secure exclusive access to a mate, but also to bring competitive advantage to pair members in acquiring resources for breeding and survival. Since the book was published in the 1996, substantial advances in the understanding of pair bonds and their dynamics has occurred. Research so far has been centred mainly around breeding success correlates and broad scale life-history, demographic and environmental correlates of fidelity and divorce. However, there are still significant gaps in our knowledge about these commonly studied aspects of pair bond dynamics. Further, there are several areas related to pair bond stability (e.g. the impact they have on survival) that remain largely neglected. Thus, the main motivation of my thesis was to fill in some of these gaps, and to address and find solutions for several important topics (and issues) that need further consideration. Filling these gaps in our knowledge has provided a more comprehensive understanding of the causes, process, and consequences of pair bond dynamics, as well as the evolution and maintenance of social monogamy.

Pair fidelity, divorce, and fitness

Stability of pair bonds (over subsequent breeding attempts, as well as between breeding attempts) can influence fitness through breeding success and survival. While it has already been well established that repeated breeding with one partner generally leads to an increase in breeding success (Black 1996), there was no consensus as to whether divorce also leads to an increase in breeding success, and whether divorce is an adaptive behavioural strategy (Choudhury 1995, Black 1996). In **Chapter 2** of this thesis, I showed that divorce is generally adaptive in terms of breeding success across 64 monogamous bird species for which data on correlation between breeding success and divorce existed. Controlling for phylogeny and several methodological moderators, I showed that divorce is triggered by low breeding success, and that it leads to a positive change in breeding success. The results of my analysis yielded several other insights into the costs and benefits of divorce. First, I have detected that the earlier breeding stages (laydate and clutch size), but not the later ones, can predict divorce. Pairs that start to breed later, and pairs with a lower clutch size, were more likely to divorce to the next breeding season. It is likely that selection would favour the decision to divorce to be based on those components of breeding success over which individuals have more control (Lindstrom 1999). Although later stages of the breeding cycle reflect partner quality (e.g. ability to provide for the chicks) too, they are, at the same time, more likely to depend on stochastic external factors (e.g. predation, or bad weather). As such, they should not be reliable cues on which to base the decision of whether to divorce. However, at the same time the decision to divorce might depend on the prospects of improved breeding success (Choudhury 1995). I detected that laydate and brood level measures (hatching success and number of hatchlings) might be more important than the other components in this respect, as they showed a positive increase as a result of divorce. This finding does not clash with the ‘stochastic environment’ theory: in the first case the decision is based on the current reproduction only, while in the second it involves the assessment of the prospects of finding a better partner, which is likely not based on completely the same cues. Interestingly, and in line with a relatively broadly accepted hypothesis that females might more often initiate divorce (Choudhury 1995, Cezilly et al. 2000), I found that females, but not males, improved in laydate and brood level measures.

In **Chapter 2** I also detected a possible reproductive cost of divorce - skipped breeding: divorced birds skipped breeding more often than widowed or faithful birds. It is not surprising that birds that have lost their partner (either as of divorce or partner death), and are thus faced with the problem of finding a new one, skip breeding more often than the faithful birds. However, the interesting finding from my analysis was that divorced birds skipped breeding seasons more often than widowed birds. If skipped breeding is a choice that balances trade-offs between the current and future reproduction (residual value hypothesis, Coulson 1984, Aebischer and Wanless 1992), then divorce participants might be birds that have actively chosen not to breed, while widowed birds still try to (and sometimes successfully do so) obtain a new partner after the previous partner had died. On the other hand, if divorced birds are the 'victims' of divorce (i.e. left by their partners), and likely to be of a low quality, they may have difficulties in obtaining a new partner (Ens et al. 1993). The frequency of skipped breeding might well have been underestimated in my meta-analysis, as studies on wild birds usually do not detect skipped breeders, but consider these birds to be dead. In **Chapter 5** I solved the recapture problem (using a framework I developed in **Chapter 3)** and looked in more details into the cost of skipped breeding in a mute swan colony. In accordance with the results from **Chapter 2**, I found that faithful birds do not skip breeding, while birds that have not kept their partners (either because of windowing or divorce) suffer a substantial cost. I also found that the likelihood to skip a breeding season was related to sex (i.e. males > females), and stage of breeding lifetime (i.e. females between their 1st and 5th breeding season > older females). This heterogeneity indicates that different individuals face different pressures on mating outcomes (regardless of whether skipped breeding is a choice or not).

The important component of fitness that the studies on the adaptiveness of secondary mating outcomes rarely address is survival. This is, at least in part, caused by the difficulties in distinguishing between those individuals that are dead, and those that are not captured. Thus, to overcome this (and some other problems I address later in the discussion), in **Chapter 3** I developed a probabilistic multievent capture-mark-recapture (MECMR) framework that simultaneously addresses survival and fidelity rates, while explicitly accounting for imperfect detection, capture heterogeneity, and uncertainly in the assessment of pair status. Using this framework, in **Chapters 3, 4** and **5** I showed that survival is linked to pair fidelity and partner change in three different species, great tits, blue tits, and mute swans. In all of these species I found that males and females that have changed partners had lower survival to the next breeding season compared to faithful birds. In the long-lived mute swans this difference in survival (and especially as I found it to be more pronounced in younger compared to older females) indicates that costs in terms of life-time reproduction could be quite substantial, and likely strongly select for high rates of fidelity to a partner in mute swans. Given a quite large difference in life-history traits of great and blue tits compared to mute swans, my results indicate that the survival-fidelity correlates might be widespread across different bird species, and need to be taken into account when studying fitness consequences of pairing outcomes.

The initial mate choice and secondary mating strategies

The functional significance of divorce in socially monogamous species comes from the constraints imposed by the need for bi-parental care. Because in general both partners are needed to successfully raise offspring, the only way for individuals of these species to gain the benefits of mating with a different partner is through extra-pair mating, or through changing partners between two breeding attempts (Johnston and Ryder 1987, Moller 1992, Sullivan 1994, Choudhury 1995, Botero and Rubenstein 2012). It is important to note that we do know that there are frequently benefits of repeated breeding with the same partner. However, these might not apply to all individuals, and some individuals might be better off by divorcing their partners (i.e. to increase the genetic diversity of the offspring, and/or to correct for a suboptimal social partnership). In social animals, the social environment in which the initial mate choice happens is likely to pose constraints on individuals, who might not be able to realize their preference for a certain partner. However, these constraints on mate choice are difficult to study, especially in wild populations. In **Chapter 6** I used detailed data on social association in winter flocks of great tits (tracked using a novel marking and tracking technology) to show that the social environment in which a pair has formed, and the preference expressed for the future partner within this environment, can predict the probability of a pair to divorce. Interestingly, it was the male's but not the female's social situation that predicted the divorce probability: males that had more female associates in the winter of pair formation, and males who had their future breeding partner ranked lower amongst their female friends were more likely to divorce later. Low rank of the future partner probably reflects that male choice was constrained, preferred partnership not realized, and thus dissolved later. This result adds to mounting evidence of the importance of male (and not only female) choice in socially monogamous species with bi-parental care (Johnstone et al. 1996, Clutton-Brock 2009).

Individual covariates of fidelity and carry-over effects of mating outcomes

Another interesting component of mating outcomes is that they can impact future matings, and these carry-over effects can largely influence the life-time fitness of individuals, as well as population dynamics (Berec and Boukal 2004, Maxin and Berec 2010). I detected these effects to occur through the influence of the current pair status on the future one (**Chapters 3, 4**, and **5**), and through the extended influence of the social environment in which a pair has formed on the later divorce probability (**Chapter 6**). I showed that male and female great tits (**Chapter 3**) and mute swans (**Chapter 5**) that were previously faithful to their partners had a higher probability of staying faithful in the next breeding season than did birds that had already changed their partners. In **Chapter 6** I was able to predict the future divorce probability of a great tit pair from the number of female associates a male had in the winter prior to the first breeding of the pair. A growing number of studies show that social experiences have an influence on fitness in later time periods (McDonald 2007, Gersick et al. 2012, Stanton and Mann 2012, Gilby et al. 2013). Because breeding success and survival, as I show in **Chapters 2, 3, 4,** and **5,** are often affected by secondary mating outcomes, the constraints on the initial choice acting through the social environment can have an influence on fitness beyond the breeding season following the initial mate choice.

In long-lived mute swans I was able to further explore the reasons for the heterogeneity in fidelity rates within the population. I detected that, apart from the previous mating outcome, fidelity depended on the stage of breeding lifetime in both sexes, breeding longevity (i.e. number of seasons elapsed between first and last breeding) in females, and immigration status of males. I also found that lower future fidelity rates for those birds that have already changed partners come mainly as a result of higher divorce rates of these birds, and not due to mate loss due to mortality. Interestingly, although one of the commonly suggested reasons for divorce is the low quality of a breeder (‘better choice’ hypothesis, Choudhury 1995), I did not detect any differences in the overall fidelity rates in male and female swans according to the proxy for quality – breeding longevity. However, the finding that fidelity rates drop with age in males, and at the end of the breeding lifetime in long-lived females, indicates quality might still influence fidelity, if quality is not a fixed trait, but changes through the individual’s lifetime.

Benefits of pair familiarity before the first breeding

As I have shown in **Chapter 6**, the period of the initial pair formation can impact later fidelity to a partner, likely by posing constraints on the initial mate choice. I was further interested in this period as it can reflect time-constraints on the initial mate choice, as well as act as the period of the prolonged partner assessment. In addition, the ‘mate familiarity’ effect (Tinbergen 1959, Black 2001), which is often considered as one of the main drivers of pair fidelity (Black 1996), might just as well act through pair members associating with each other prior to their first breeding. However, these options remained largely unexplored in previous studies on divorce and the ‘mate familiarity’ effect. In **Chapter 7** I detected benefits of a longer winter association period of future breeding pair members to the breeding success of a pair in the coming breeding season, however in some of the studied years. In three out of five years pairs that were detected to start associating earlier in winter started egg-laying earlier, and had higher fledging success. However, I did not detect any direct influence of this period on the future divorce probability. Still, divorce probability could have been affected by the timing of pair formation indirectly, as it was correlated with laydate and clutch size (i.e. pairs with a later laydate and smaller clutches were more likely to divorce). These results imply that there might be a selective advantage for a new pair to start associating earlier in winter, and that the benefits of pair familiarity in socially monogamous birds might come through a longer time of association prior to the first breeding of a pair.

Methodological advances and advice for future studies

As a result of this thesis, I developed a methodological approach that can be used to address a wide range of questions on pair fidelity. Moreover, based on the results from various chapters, I can suggest several important considerations for future studies on the adaptiveness of divorce and fidelity.

In **Chapter 3**, I developed a probabilistic multievent capture-mark-recapture (MECMR) modelling framework that allows for survival and fidelity rates to be addressed simultaneously, while explicitly accounting for imperfect recapture, heterogeneity of recapture among individuals, and incorporating uncertainty in assessment of pair status. I showed, in the simulated data-set, that this framework estimates state-dependent survival and pair fidelity rates under varying levels of state-dependent recapture rates better (i.e. more accurately and robustly) than the traditional method (i.e. that bases conclusions on only those individuals that are captured). In addition, the approach provides (in its current form or via simple extensions) a statistically rigorous framework for testing a range of hypotheses on the drivers of pair fidelity, including their consequences for fitness. For example, external covariates (e.g. population density, average temperature), and individual covariates (e.g. immigration status, **Chapter 5**) can be easily added to the model selection. Further, the MECMR model of pair fidelity can be applied to other types of dyadic interactions (e.g. the parent-offspring relationship, dynamics between individuals and locations, or individuals and groups). This modelling framework could be also used to address the questions on pair bond dynamics between two breeding seasons, when individuals are repeatedly detected in winter, such in the data on social associations I have looked at in **Chapters 6** and **7**. For example, it would be possible to model when mortality happens in relation to dissolution of pair bonds in winter.

The results of the meta-analysis in **Chapter 2** raised several important considerations for studies that use breeding success to address the adaptiveness of mating outcomes. My results showed that the magnitude of the detected correlation between breeding success and divorce greatly depends on the methodological approach used. For example, while there was no overall significant improvement in breeding success as a result of divorce, when I controlled for methodological moderators I detected a very strong effect (r = 0.637; 95% CI = 0.328-0.817) for the improvement of breeding success at the level of brood for females. First, dichotomising breeding success into success vs. failure should be avoided. Second, breeding success should be measured both before and after divorce. Measuring success after divorce only can lead to inaccurate conclusions as partner change (but not divorce *per se*) might be costly. In line with this, it is also be important to take into account the pairing class to which divorced birds are compared (i.e. to widowed or to faithful birds). Next, and especially in long-lived species, breeding success should be measured over multiple years. In the first year after divorce the general costs of partner change might outweigh the benefits of pairing with a better partner, and the benefits could then become apparent only in later seasons.

The lack of (the expected) influence of life-history traits on the correlation between breeding success and divorce from **Chapter 2** highlighted the need for better and more detailed data on life-history traits. Needless to say, a more comprehensive data-set on life-history traits, both in quantity (i.e. more species), as well as in quality (i.e. more precisely defined range of possible values) is needed. For example, treating species as either precocial or altricial is likely to oversimplify the full range of chick dependence on parental care, and possibly lead to the loss of detectable effects. Second, while some life-history traits are fixed for a species (e.g. developmental mode), some are very variable (e.g. site-fidelity, degree of coloniality) and likely to depend on population-specific factors. As such, defining, for example, species' site-fidelity might be based on only a small number of populations, and meaningless to relate to species-level divorce rates.

Interestingly, survival has been generally neglected as a possible consequence of pairing outcomes. This means two things: first, all of those birds that have died (i.e. had breeding success zero) won't be taken into account when studying the breeding success consequences of divorce. Second, some of the birds considered as being widowed might actually be divorced first, but their partner has died as a consequence of that divorce. Both of these are likely to lead to misleading conclusions on the adaptiveness of divorce. Mortality is difficult to study in natural populations, but with the development of new statistical approaches (e.g. **Chapter 3**), as well as better technologies to track individuals, this might become possible.

In **Chapters 3, 4**, and **5** I showed that biased recapture rates and uncertainty in pair status assignment must be taken into account when studying fidelity correlates (i.e. environmental, demographic, and individual level factors) and their fitness consequences, as they can greatly influence fidelity estimates, even in populations with high recapture rates (i.e. mute swans in **Chapter 5**). For example, problems can arise when comparison of fidelity rates or fitness consequences is done based on types of individuals (e.g. age) that also differ in capture probability.

Finally, given that some species (or populations) exhibit time-varying rates of fidelity (e.g. great and blue tits in **Chapters 3, 4**, and **5**), studying species-specific pair fidelity rates in relation to large-scale environmental factors, or species life-history traits, should ideally be based upon assessments of fidelity rates over several years, or at least control for the length of the study period over which fidelity rates were taken.

Final remarks on social and genetic monogamy, pair bonds, fidelity and divorce – call for a unified framework

Having spent almost four years working on the question on stability of pair bonds in socially monogamous species, I have repeatedly encountered several conceptual problems that complicate understanding and studying functional (i.e. fitness) significance and direct external influences (e.g. demography of a population) on pair bond dynamics.

First and foremost, it is important to distinguish between pair bond, social monogamy, and genetic monogamy. The easiest way to define these three main concepts (and where they overlap) is by combining three other, simpler concepts: reproduction (i.e. mating and producing offspring), exclusivity (i.e. shared between only two individuals), and cohabitation (i.e. sharing a territory or other resources). I represent this framework in Figure 1. For example, exclusive reproduction leads to genetic monogamy (but not social monogamy), while (non-exclusive) reproduction with cohabitation leads to social monogamy. What is important to notice here is that pair bond does not require reproduction, and that social monogamy appears only when pair bond is connected to reproduction. These concepts are important to distinguish as they have overlapping (but not identical) evolutionary origins and functional significance. For example, benefits (and costs) of pair bonding can exist without reproduction, or within other social mating systems.

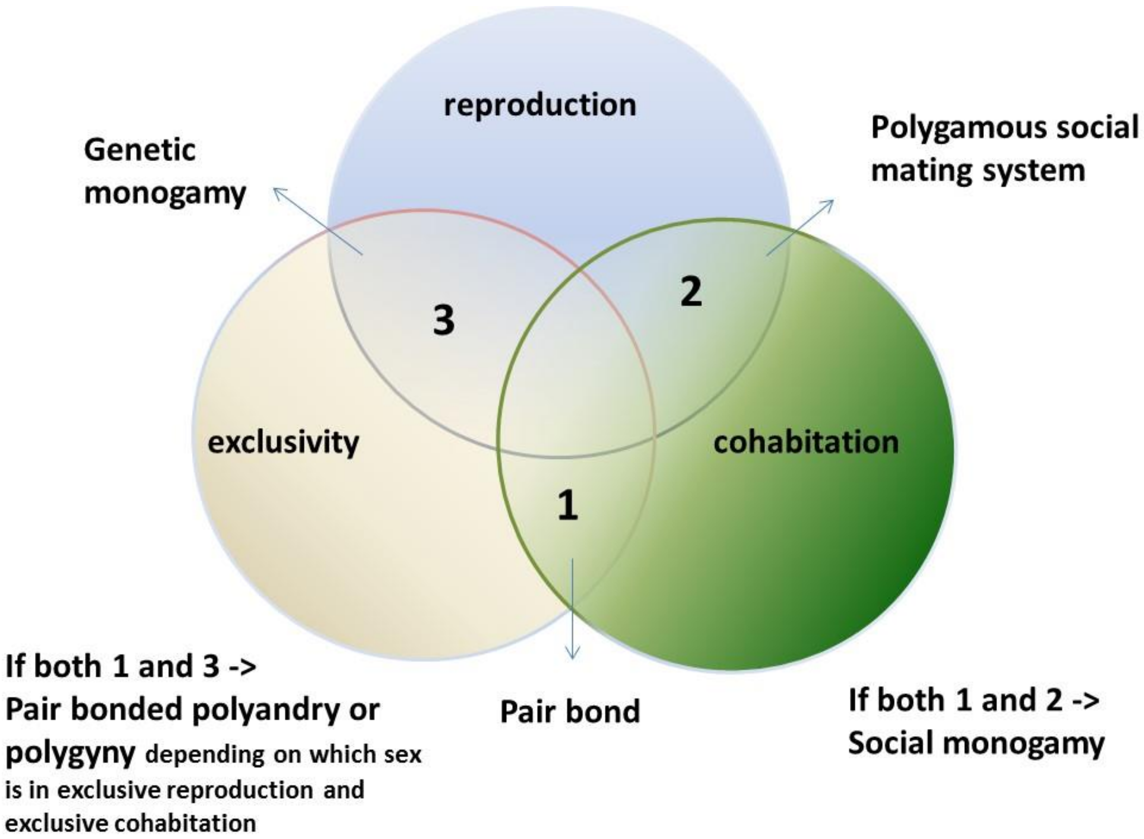

Figure 1. A simple representation of the framework to define pair bond, social monogamy and genetic monogamy. This framework uses three main basic concepts: exclusivity, reproduction, and cohabitation; combining these in different ways defines mating systems and pair bond. Costs and benefits of the overlapping areas of the basic concepts (1,2, and 3) are important to consider when addressing evolutionary and functional significance of pair bonds, pair bond stability, and social and genetic mating systems.

This leads to another important consideration: pair bonding exists without reproduction, and this is often neglected in studies on social monogamy in birds. I believe that this has arisen because in humans social monogamy is usually defined regardless of whether a pair reproduces or not. However, in birds in seasonal climates there is a distinctive period of reproduction (i.e. breeding season), which can (but does not have to) be followed by cohabitation outside of the breeding season. Thus, the benefits of pair bonding within the breeding season (e.g. bi-parental care) are not the same as the benefits of pair bonding outside the breeding season (e.g. pair might be more competitive), and the dynamics of pair bonds should be considered within this framework. This also relates to the concepts (again, often interchangeably used) of continuous vs. part-time partnership, and long-term vs. short-term partnership. The first two concepts describe whether a pair bond is maintained in the period between the two breeding seasons, while the second two describe whether a reproductive pair bond is re-established in the subsequent breeding attempts.

Finally, in animal behaviour, divorce is currently defined based on what happens within pairs between two subsequent breeding seasons, and as such relates to the concepts of ‘cohabitation’ and ‘breeding’ (Fig 1). However, if we consider divorce from the perspective of pair bond (i.e. ‘cohabitation’ + ‘exclusivity’) than broader definitions are conceivable. For example, in resident species, it might be possible to define divorce as having occurred when a marked change in social affiliation occurs in the period between the two breeding seasons. Exploring divorce in this context would give important insights into the evolution of pair bonds and social monogamy in birds.

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