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# Causes of divorce in long-term monogamous bird species

*What causes divorce in long-term monogamous bird species and what are its fitness consequences?*

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**Bachelor Thesis Evolutionary Ecology**
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**Abstract**

The existence of social monogamy in birds could be due to the need for male parental care, the temporal distribution of the females, spatial distribution of resources or female-female aggression. Within social monogamy, an extraordinary variation has been found: long-term monogamy. The sole fact that this kind of monogamy exists means can be beneficial for individuals. However, divorces between individuals have been observed. This literature study will try to determine the causes and consequences of divorce in long-term monogamous birds. Four main hypotheses have been posed in an attempt to find a cause for divorce: the incompatibility hypothesis, the better option hypothesis, the accidental loss hypothesis and the forced divorce hypothesis. Some studies claim to have found evidence for the incompatibility hypothesis as well as the better option hypothesis to be the cause of divorce, but one has to question whether these two hypotheses truly differ from one another. Even with these indications, other studies, although on different species, contradict these results. When regarding the accidental loss hypothesis, again contradictory results are found. Research concerning the forced divorce hypothesis mostly has found evidence for this hypothesis. One can question whether the accidental loss hypothesis and the forced divorce hypothesis are proximate explanations, or the mechanism through which an ultimate process takes place. Even though there are several factors complicating a conclusion on the cause of divorce in long-term monogamous birds, I suggest that there is only one cause for divorce: when there is a possibility to improve reproductive success, divorce will take place. I stress that it is not important if this is due to the incompatibility hypothesis, the better option hypothesis, the accidental loss hypothesis or the forced divorce hypothesis, since in the end divorce always results in a (relatively) improved reproductive success.

**Introduction**

The Bewick's Swan (*Cygnus colombianus bewiickii*) is a small swan species that mainly breeds in the Arctic and subarctic tundra. They migrate up to 4000 km every year to their wintering sites that are mainly located in the Netherlands, Britain and Ireland (Rees *et al.*, 1996). This species is known to be long-term monogamous. In Welney, Norfolk, an extraordinary pair of Bewick's Swans has been observed (Rees *et al*., 1996). The pair had been together for seven years when they divorced. On the first sight, this is not very special, since divorce has been observed in several long-term monogamous species. What makes them so extraordinary, is that during their pair bond of seven years they did not produce any offspring (!). After the divorce, the female has been seen for three or four years with a new partner, successfully breeding. The male, however, was seen for two more years without repairing. Why did these two swans stay together for seven years, while they did not produce any offspring? Why did they suddenly choose to divorce? Was it even a choice of these former partners or was their divorce the result of other, unknown factors influencing their pair bond?

These and other questions are raised when looking at the concept of monogamy in birds species. The term monogamy, however, can refer to social or genetic associations (Gowaty, 1996). When regarding social monogamy, it is meant that one male and one female form a pair bond, a male-female association at any time of year, especially during breeding season while they do not per se only copulate within this pair bond. This can also be called one-male one-female groups (Black, 1996). Genetic monogamy however indicates that only fertilization occurs between one male and one female, while the individuals not necessarily stay together for a certain period. Then there are socially monogamous species in which the pair bond only lasts one year, but also in which the pair bond lasts for more years, sometimes even exists for a lifetime. The last is called long-term monogamy. When the term divorce is used, it is meant that the pair splits up and at least one partner has repaired with another individual while both are still alive (Choudhury, 1995).

Although over 90% of all birds is socially monogamous (Choudhury, 1995) and of this 20-25% is genetically monogamous (Birkhead & Møller, 1992, cited by Gowaty, 1996), its origin and consequences are still hardly understood. When looking at the possible mating systems, one would expect polygyny to be the most prominent: for a male, fertilizing multiple females would be advantageous, since increasing the number of offspring increases reproductive success (Davies, 1989). A female however would benefit from a partner with high (genetic) quality which helps with raising the offspring (male parental care). This means that a female favors monogamy, while in general a male favors polygyny.

Monogamy as a mating system seems to be the result of constraints rather than of possible advantages (Black, 1996). It is hypothesized that the "decision" for monogamy depends on several factors. The need for male parental care seems to play an important role. When male parental care is required for successful rearing of the young, the species automatically has obligate monogamy as a mating system (Davies, 1989). However, in several monogamous species it has been observed that male parental care is not absolutely necessary (Gowaty, 1996). Three other hypotheses have been posed to explain monogamy in these species. Temporal distribution of the females is of great importance (Gowaty, 1996). When females breed simultaneously, this makes polygyny difficult for a male since he cannot be on multiple places at the same time. The spatial distribution of resources is

another factor. When a male is unable to defend more resources than the resources sufficient for one female, polygyny is not an option. Third female-female aggression may prevent polygyny because the resident female does not allow other females in her territory. (Gowaty, 1996)

For some species long-term monogamy seems to be more advantageous than other mating systems. The level of fidelity of a breeding pair is dependent on the life span and the mortality of a species (Black, 1996). Mate fidelity and life expectancy are positively correlated (Bried *et al*., 2002). When a species has a low life expectancy, the costs of establishing a long-term pair bond are not compensated by the advantages on the long term, which include an increasing reproductive success over the duration of the pair bond: in Barnacle Geese (*Branta leucopsis*) it was found that reproductive success increases during the first seven years of the pair bond (see figure 1; Black *et al.*, 1996; Ens *et al*., 1996; Black, 2001) while the average age of a Barnacle Geese is eight years. The same also has been found in several swan species: their reproductive success increased with pair duration during the first 11 years in Bewick's swans, 6 years in Wooper Swans and 5 years in Mute swans (Rees *et al.*, 1996). When a species has a high mortality rate, a partner may not wait long for its mate to return, since the chance of its return is small. Thus the partner will search for a new mate sooner (Black, 1996).

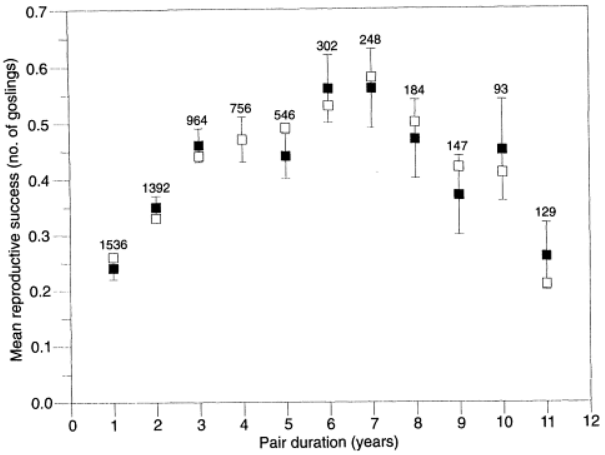


***Figure 1.*** *Relationship between pair duration and reproductive success in Barnacle Geese (n=6297 pair-years). Filled squares are the observed means and their SE. Open squares represent the fitted values of log-linear models after controlling for year and female age. Reproductive success varied significantly with pair duration (ΔD = 49.0, Δdf = 1, P<0.001). The quadratic function of pair duration was also significant (i.e. duration$^2$, ΔD = 39, Δdf = 1, P < 0.001), as was the interaction between pair duration and year (ΔD = 43, Δdf = 16, P<0.001) meaning mate familiarity may have been more useful in some years than others. Figure and subscript abstracted from Black* et al*., 1996.*

A long-term monogamous pair bond means increasing coordination and cooperation between pair members, longer parental investment of both parents and less costs in general for both pair members, since they do not have to search for a new partner (Black, 1996). The search for a new partner brings costs like possible injury, predation or even failing to find a suitable mate and thus missing the breeding season. An example of this last is found in Barnacle Geese (*Branta leucopsis*): Barnacle Geese take 3-9 months to select a new mate, which means they risk missing a breeding season by searching a new mate (Black *et al.,* 1996).

For the female, a long term pair bond can even be essential. In multiple species, for example ducks, geese and swans, males defend females and the territory against imposters (Black, 1996). Because of this, the female does not have to spend her energy on the defense of herself and the territory and this enables her to build up fat and nutrient reserves for breeding. This improves reproductive success. The male also defends the eggs and the territory while the female takes incubation breaks, which ensures that the female can breed successfully (Black, 2001; Black, 1996). To do this, the pair members have to maintain contact and have a good coordination between pair members. This coordination increases over the duration of the pair bond (Black, 1996).

But when long-term monogamy has so many advantages, then why is it observed that pairs divorce? Mate loss as well as divorce when both partners are still alive, comes with consequences. For example, Nicolai et al. (2012) found that when Black Brent Geese lost their partner through harvest, this made the remaining partner more vulnerable to harvest and possibly even to natural predation.

Nowadays it is mostly believed that divorce in socially monogamous birds is a choice to increase its fitness and that birds continuously have to decide whether to stay with their current partner or to divorce and search for a new partner (Choudhury, 1995), but until now only indications have been found. This leads to the main question of this literature study: what causes divorce in long-term monogamous bird species and how does this affect their fitness? Four main hypotheses on the causes of divorce will be discussed. Other hypotheses, as stated by Heg *et al*. (2003, cited by Jeschke *et al*. (2007)), can be considered as proximate variations on these hypotheses and thus will in this study be considered as such.

**Fitness effects of divorce**

When divorce is a decision to improve reproductive success, one would expect the individuals that make this decision to gain advantages. Since costs also come with divorce (see below), the advantages must outweigh the costs. It is also thought that even when divorce is not due to a decision of one of the partners, but has been forced or the individual has accidentally lost its mate, divorcing still is advantageous compared to not divorcing. For example, when an individual is forced to divorce by an intruder, it is very costly to keep fighting with this intruder. Staying and keep fighting means higher costs for the individual than the costs of finding a new partner. When losing a partner accidentally, waiting for the partner to return may also be more costly than choosing a new partner (Choudhury, 1995).

In Barnacle Geese (*Branta leucopsis*) the time until repairing after divorce is on average 3-9 months (Black *et al*.,1996). This means that when an individual decides to divorce, it takes the risk of missing a breeding season and thus have no reproductive success in that year, which heavily influences the individual's fitness. Also, when divorcing, the geese take the risk of repairing with a younger, inexperienced partner since a high percentage of the non-breeding population are young geese (Black *et al*.,1996) which could also lead to low reproductive success. Black *et al*. (1996) also found that geese that changed mate had a lower chance in the first year after divorce on returning with a gosling the next year compared to those that did not change mate. In the second and third year on the contrary, the difference disappeared. This means that at least in Barnacle geese, divorce comes with risks and fitness consequences.

In oystercatchers (*Haematopus* ostralegus) different fitness consequences have been found depending on the territory type and divorce type (Heg *et al*.,2003). One can distinguish residents and leapfrogs: residents live close to the foraging areas, while leapfrogs have a territory further inwards, which forces them to cross longer distances to the foraging areas. Two kinds of divorce have been observed: divorce by desertion of one of the partners and divorce by usurpation (Heg *et al.*, 2003). The fitness consequences of divorce differed depending on the kind of divorce. The future lifetime reproductive success has been predicted for the individuals by Heg *et al* (2003). It was found that for leapfrogs future lifetime reproductive success increased for deserters and decreased for the victims of desertion and usurpation. However for residents all birds that divorced, except for the bystanders (the birds that are claimed as a partner by an intruder) the future lifetime reproductive success only decreased, including the deserters. One however could question these data, since although it is based on measurements, these data are estimates of future lifetime reproductive success.

When regarding these studies, it is suggested that divorce comes with fitness consequences. However, data on the fitness effects of divorce in other species are very scarce, which makes it difficult to analyze fitness consequences of divorce in general. The sole fact that divorce occurs however, indicates that it at least on the longer term has beneficial effects too. However, the study of Heg *et al.* (2003) only covered 15 years of observations, while some of these birds reach an age of 40. This means that for the average aged oystercatcher the bigger part of its life has been recorded, but there are also individuals of which the effects on the longer term have not been measured since they grew older than the timespan of the study. This could indicate that true long-term research on the fitness effects on divorce may not exist.

While one still has to consider all limitations to the known studies on fitness consequences, these studies indicate that divorce does come with fitness consequences on lifetime reproductive success. This means that, as stated by Choudhury (1995), birds continuously have to consider whether to stay with their old mate or to divorce and pair with a new partner. The trade-off between the costs of divorce and the costs of staying is crucial in this decision.

**Hypotheses to improve reproductive success**

When regarding the possible causes of divorce, one can distinguish hypotheses concerning ultimate explanations and hypotheses concerning proximate explanations. The hypotheses concerning ultimate explanations mainly regard hypotheses that assume divorce as a choice of an individual to improve its reproductive success (Black, 1996). These are the incompatibility hypothesis and the better option hypothesis. The hypotheses concerning proximate explanations mainly regard divorce by circumstances: the accidental loss hypothesis and the forced divorce hypothesis. (However, one can argue that these proximate explanations eventually are part of an ultimate explanation. This difficulty will be addressed in the next chapter).

*The incompatibility hypothesis*

Coulson (1972, cited by Black, 1996) proposed the possibility of compatibility or complementarity of the pair members to have an effect on their fitness. From these thoughts the incompatibility

hypothesis was extracted: divorce could occur when a certain pair combined had a low reproductive success. Although these individuals apart are not necessarily of low quality, together they have a reduced fitness (Choudhury, 1995). One would expect both individuals to gain advantage from divorce, since it would mean the possibility of finding a better suited mate for both (Choudhury, 1995).

A derivative of this hypothesis is the error of mate hypothesis. It is stated that when a bird chooses its mate, it does not have all available information on all possible mates and also it does not have access to all mates (Real, 1990; Sullivan, 1994). When this bird has to continue its search for the perfect partner, this could bring high costs with it. On some point the individual has to decide on a mate whether it has all necessary information or not. This is why the bird is expected to not get the best mate possible. The pairing process of Barnacle Geese (*Branta leucopsis*) could be an example of this. It is known that Barnacle Geese sample one to six possible mates by entering trial partnerships, which mostly last up to several weeks (Black *et al*., 1996). Using the information gained from this trial partnerships, they decide on which one will be their true mate. The error of mate hypothesis states that divorce occurs because of an error has been made when choosing the original mate (Black, 1996) and thus is a form of incompatibility which was not noticed when choosing the initial mate.

There are some indications for compatibility or complementarity to influence reproductive success. Black *et al.* (1996) showed that reproductive success was optimal when an individual paired with a mate of similar size (see figure 2). Mating with an individual of greater or smaller size decreased reproductive performance. It has been hypothesized that this is due to higher stress for small females during social interactions with large males, which could inhibit the flow of reproductive hormones (Greenberg & Wingfield, 1987, cited by Black *et al*., 1996).

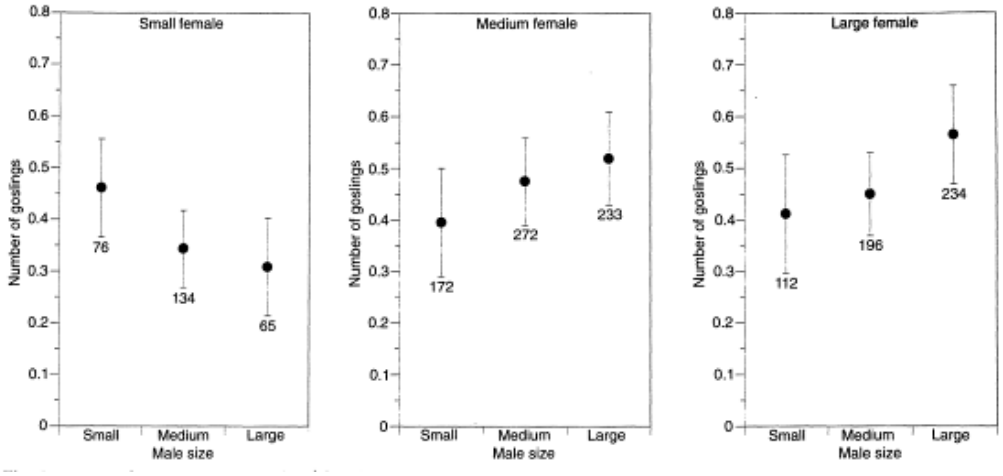


***Figure 2.*** *Reproductive success in Barnacle Geese (the number of goslings, and SE bars) of different pair-size combinations. Barnacle Geese maximized production of goslings when paired to a mate of similar relative body size; pair-size significantly influenced overall reproductive success, after controlling for year and age effects (ΔD = 21.5, Δdf = 8, P<0.01). Size categories were based on the first principal component (PC2) derived from skull and tarsus measures. Medium-sized birds were within half a SD of the mean, small birds below and large birds above this. Figure and subscript abstracted from Black* et al.*,1996; derived from Choudhury, 1996.*

When a pair divorces due to incompatibility and low breeding success, one would expect that divorce rate is related to breeding success: the higher the breeding success, the lower the divorce rate. Ihle

*et al*. (2012) revealed that female zebra finches (*Taeniopygia guttata*) that experienced repeated hatching failure were not more responsive towards other males in comparison to females that experienced a high hatching success. Although this experimental study focused on possible extra-pair contacts where the pair bond stayed intact and not specially on mate fidelity, this is an indication that the incompatibility hypothesis does not explain divorce. Research of Black *et al.* (1996) also revealed that the incidence of divorce was not significantly higher in pairs that failed to reproduce compared with pairs that successfully reproduced. This corresponds with results found by Coulson (1972, cited by Choudhury, 1995) in Kittiwake (*Rissa tridactyla*), where no correlation was found between breeding success and divorce rate, and the results found by Rees *et al.* (1996) in Whooper Swans, where also no correlation was found between the frequency of divorce and the reproductive success.

*The better option hypothesis*

The better option hypothesis states that the availability of a higher quality mate is a cause for divorce. To improve its reproductive success, one of the partners will initiate divorce and form a pair bond with this higher quality mate (Davies, 1989). This idea originally was thought of by Baeyens (1981; cited by Black, 1996) who suggested that one member of the pair may initiate the divorce when it has a better partner available and therefore making its old partner a victim. One thus would expect only the partner that initiated the divorce to gain advantages, since only the initiator 'upgrades' its mate and its former partner is left as a victim (Choudhury, 1995).

Several studies have tried to provide insight in the value of this hypothesis. For example, Black (1996) suggested that Barnacle Geese only switch partner when one of higher quality is available. Getting a new mate when one of higher quality is available results in a higher reproductive success (Ens *et al*., 1996). This would mean that having more partners would improve lifetime reproductive success, since each following partner is an upgrade compared to the last one. Black (2001) however found no difference in reproductive success between Barnacle Geese with more than two partners and Barnacle Geese with one or two partners. This outcome corresponds with results of Black (2001), who states that Barnacle Geese had a higher lifetime reproductive success when being monogamous.

Dhondt and Adriaensen (1994) suggested that divorce in Blue Tits is also caused by the availability of a better mate. In their research, they found that the female had an increased reproductive success (see figure 3) in the year following the divorce, whereas the male did not differ in reproductive success between the two years. This is as expected to follow from the better option hypothesis, since it predicts one of the partners to have an advantage from divorce and the other one to be the victim. However, the Blue Tit is only known to be monogamous on the short term. One could discuss whether a long term partnership is even possible in this species, since it is much more short lived compared to other species used in this literature study.

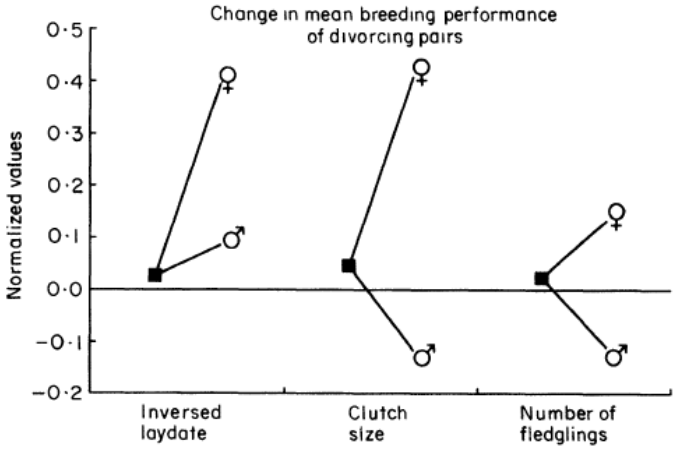


***Figure 3.*** *Mean breeding performance in Blue Tits (normalized values for laydate, clutch size and number of fledglings) of pairs that will divorce (squares) and of both members of the pair separately in the following year. In order to show all improvements as positive values the inversed laydate (laydate*-1) is used. A one-way ANOVA (df = 131) on breeding performance in the year after divorce, with sex as a factor, showed that divorced females had a significantly larger clutch than divorced males (F = 8.96, P = 0.003). The same trend was also found for laydate and number of fledglings (laydate: F = 3.42, P = 0.07, number of fledglings: F = 1.42, P = 0.24). For laydate and clutch size, females, but not males, did significantly better than the population average of zero (t-test: α = 0.05). Figure and subscript abstracted from Dhondt & Adriaensen, 1994.*

In oystercatchers divorce by desertion of a partner has been observed. Heg *et al.* (2003) found that victims of divorce in high-quality territories lost more fitness than victims of divorce in territories of low quality. Combined with the observation that extra pair partners can become social partners of the oystercatchers through divorce (Heg *et al.*, 1993, cited by Heg *et al.,* 2003), they suggest that the better option hypothesis is most likely to explain divorce by desertion.

Pérez-Staples *et al.* (2013) observed divorce in the Blue Footed Booby (*Sula nebouxii*). In five out of seven pairs, the male deserted the female. However, there was no evidence of contact between these males and their new partner when the males were still with their old partners. This rules out the better option hypothesis in these cases, since when a new partner is found after divorce, it could impossibly be the initiation of the breakup.

*Disentangling the hypotheses?*

Even though the incompatibility hypothesis and the better option hypothesis are seen as hypotheses that come up with different causes for divorce, I found it hard or even impossible to use observations to distinguish between the incompatibility or the better option hypothesis (Choudhury, 1995).

The difference between these hypotheses is rather subtle. When pair members would be incompatible, both would benefit from divorce and having a new mate and thus the divorce would be initiated by both pair members. When for one partner a better mate is available, this would mean that the initiation of the break-up is one-sided (Pérez-Staples *et al.*,2013). However, an incompatible pair may not directly split up when no other partners are available, since it would be better to have an incompatible mate than no mate at all (Choudhury, 1995). This means that when for one partner a

better mate is available, this can also lead to their breakup, so even when regarding incompatible pairs, divorce may still be the result of a one-sided initiation.

From this another factor can be deduced that makes the disentangling of the two hypotheses nearly impossible. One can argue that when a better mate is available for a pair member, this means that the initial pair was relatively not compatible – otherwise, there would not have been a better partner for this pair member. Vice versa, one can argue that when two partners are incompatible, for example by body size(see '*The incompatibility hypothesis*'), a new partner is always 'the better option' for them, since having a new partner would improve its reproductive success (Choudhury, 1995). This leads to the contemplation whether there is a difference between these hypotheses at all.

Besides the question whether the better option hypothesis and the incompatibility hypothesis can be seen as two separate hypotheses, the incompatibility hypothesis itself still has its limitations. The incompatibility hypothesis states that when reproductive success is low, divorce occurs since this is a sign of incompatibility of the pair members. However, when the circumstances in a year are bad, this also results in a low reproductive success. One then would expect, when the incompatibility hypothesis is true, that more divorce occurs in a bad year due to the reproductive failure. But when circumstances are bad, a new mate will not give any advantages. So there should be other cues for the possible incompatibility than only reproductive success, since this is also influenced by other factors as well.

**Hypotheses related to other causes**

Two hypotheses that are related to other causes than the improvement of reproductive success, have been suggested to explain divorce in long-term monogamous bird species: the accidental loss hypothesis and the forced divorce hypothesis.

*The accidental loss hypothesis*

For migratory birds like geese the accidental loss hypothesis was constructed. It states that a temporary separation during migration, for example due to unbeneficial weather or disturbance, may lead to divorce in order to minimize (fitness) losses (Owen *et al.,* 1988, cited by Black, 1996).

Several studies have tried to find support for this hypothesis. In King Penguins (*Aptenodytes patagonicus*) for example, a significant correlation between divorce probability and asynchronous arrival has been found (Olsson, 1998). Asynchronous arrival thus is thought to be an important factor for divorce in King Penguins.

The accidental loss hypothesis however was not supported by research conducted by Rees *et al.* (1996). They observed divorce in several swan species and found that divorce was highest in Whooper Swans, of which the migration distance was shortest and no divorce was found at all in Bewick's Swans, that migrate long distances. Also in Barnacle geese the number of divorces was found to be the highest during the non-migratory winter season (Black *et al.*, 1996). This leads to thinking that at least in these species, the accidental loss hypothesis is not the cause of divorce.

*The forced divorce hypothesis*

Sometimes it is observed that a third individual approaches a pair of birds. From this observation, the forced divorce hypothesis was formed: divorce may be caused by intrusion of a third party which 'claims' one of the original pair members as its mate. Through this, it replaces one of the original pair members (Choudhury, 1995, cited by Handel & Gill, 2000).

Jeschke *et al.* (2007) claimed that in the guillemots (*Uria aalge*) the forced divorce hypothesis was the most logical explanation for their found results. They predicted that when forced divorce was the cause of a divorce, this would mean a lower reproductive success for the victim, no change in reproductive success for the other mate and an increase in reproductive success for the intruder. They also stated that the divorce rate through forced divorce would be higher in young birds, since they were supposed to have less experience in dealing with an intruder. It was found that in most cases of divorce, divorce was not beneficial for both of the original partners (data covered from 1982 up to 2005), which is contradictory to other hypotheses on divorce: both the incompatibility hypothesis and the better option hypothesis state that divorce would eventually improve reproductive success. However, it was not noted if a third party was involved in the observed divorces .

In the oystercatcher (*Haematopus ostralegus*) divorce has been observed. It was found to be quite common that an outsider intrudes on the pair members and disrupts the pair bond: divorce by desertion and divorce by usurpers occurred in similar numbers (Heg *et al.*, 2003). It starts with occasional intrusions by the intruder, also called the usurper, which eventually leads to extreme fights with the pair member of the same sex as the usurper. It was found that a victim of a usurpation had a lower future lifetime reproductive success, while the bystander (the claimed new partner of the usurper) experienced no significant differences in future lifetime reproductive success. Heg *et al.* (2003) state that these results are only to be explained by the forced divorce hypothesis.

*Ultimate or proximate explanations?*

The accidental loss hypothesis and the forced divorce hypothesis seem to have nothing more in common than that they both are proximate explanations on the cause of divorce in long-term monogamous bird species. However, it can be argued that for example the accidental loss hypothesis, a proximate explanation, could be the underlying mechanism through which the incompatibility of a pair would be expressed. When a pair of birds would be (slightly) incompatible, this could influence their decisions when migrating between breeding and wintering grounds. For example, a female could stay a little longer on the wintering grounds to gain more fat for breeding and so risk arriving asynchronous with her partner, or leaving on the same moment as her partner but may not having enough fat reserves to breed successfully. When the partner is not of high quality for this individual, one could hypothesize that in that case it is more beneficial to ensure sufficient fat reserves and risk losing its mate in the process. Since they were not completely compatible, the loss of this mate could not be that disadvantageous since it even enables the individual to eventually get a better mate.

It is thought that even when forced divorce leads to a split-up between partners, leaving its original mate could be beneficial to an individual. When the individual stays, this could bring higher costs than when it leaves and searches for a new mate (Choudhury, 1995). One could even argue that when one of the original mates is unable to defend its partner against an intruder, the intruder actually is the better option for the partner and this could be the actual cause of divorce (Jeschke *et al.*, 2007). One can also say that since the individual is not able to defend its partner, they are not as compatible as initially thought. This makes it questionable if the forced divorce hypothesis is only a proximate explanation, or the mechanism through which an ultimate explanation like the better option hypothesis takes place.

**Discussion**

There are indications that point to the direction of the incompatibility hypothesis as well as the better option hypothesis and the accidental loss hypothesis to be the cause of divorce. Even with these indications, other studies, although on different species, contradict these results. One can even argue whether the incompatibility hypothesis and the better option hypothesis are separate hypotheses at all. Evidence has been found that supports the forced divorce hypothesis. However, both the accidental loss hypothesis and the forced divorce hypothesis are thought to be part of either the incompatibility hypothesis or the better option hypothesis.

When regarding the found results, a lot of studies contradict each other. Some claim to have found evidence for one or more of the hypotheses on divorce, others seem to have revealed that one or more hypotheses can be discarded. However, two factors are of great influence on drawing a conclusion from these results. First, in most studies used in this literature study, only correlations have been found. Except for a couple of articles, most describe observations of behaviour. Almost no experimental studies are to be found on long-term monogamy in birds. One of these exceptions is the article of Ihle *et al.* (2012) concerning zebra finches, but even with this research one can argue that measuring fitness in captive held animals is not representative for free-living animals. In most studies on divorce in monogamous birds, the data were collected for other purposes (Choudhury, 1995). This means that these post-hoc analyses can be very useful, but it is hard to strictly test hypotheses through this research method, since no experimental manipulations (as said before) have taken place (Choudhury, 1995). I suggest that research concerning experimental manipulations of breeding pairs will be conducted. Through experimentally inducing, for example, a (repeatedly) lower reproductive success in a natural population and breeding area, one could study if incompatibility causes divorce in the studied bird pairs. One could even offer a better mate to a breeding pair (however, selecting a truly better mate will be a difficulty that has to be considered before conducting this research) could lead to more indications on the validity of the better option hypothesis. To test the accidental loss hypothesis, one could prevent the partners of arriving on the same moment on the breeding grounds and therefore simulating an 'accidental' loss. By 'manually' adding a competitive partner (which will try to claim one of the original partners) one could even study forced divorce in birds. However, before conducting such experimental research, the impact of these manipulations on bird populations and individuals should be researched, since it is very important that these experiments do not influence other factors of divorce or even influence population dynamics and therefore interrupt natural processes. This makes experimental studies very difficult, but hopefully not impossible. Second, studies focus on one species. In this literature

study, results from research on a number of long-term monogamous species have been used, which means that these results may not even be comparable, since it concerns different species. This immediately leads to the problem: it could be that the cause of divorce differs between species – this is actually very likely, since there is a fair amount of variation in the ecology of the used species. From this can be deduced that while the results of this literature study contradict each other, it would not make them less valid. I find it very likely that in different species different factors cause divorce of long-term monogamous pairs.

This would lead to the next question: if there could be between-species variation in the cause of divorce, could there also be within-species variation? Or even within-population variation? Jeschke *et al.* (2007) state that they found indications for different within-population divorce mechanisms. According to their results, the accidental loss hypothesis was very likely to have caused the found divorces in guillemots (Uria aalge), but also the forced divorce hypothesis.

Heg *et al.* (2003) confirm that it would be likely that there is more than one divorce mechanisms in a species. When looking at the results of their study, they state that divorce in the oystercatcher cannot be explained by a single hypothesis but needs at least two. They find it very likely that the observation of divorce by desertion and divorce by usurpation are explained by respectively the better option hypothesis and the forced divorce hypothesis (see also *The better option hypothesis* and *The forced divorce hypothesis*). In more species, indications for divorce as a result of desertion by one partner as well as forced divorce have been found: blue ducks *Hymenolaimus malacorhynchus* (Williams & McKinney, 1996) , great tits *Parus major* (Dhondt *et al*., 1996), house-wrens *Troglodytus aedon* (Freed, 1987), and great skuas *Catharacta skua* (Catry *et al.*, 1997; all of the previous articles cited by Heg *et al.*, 2003).

It can also be argued that when a species has a high site fidelity, it possible that mate fidelity results from this. When this is true, it means that divorce can simply be the result of habitat changes and instability (Choudhury, 1995). This complicates the research of the hypotheses on divorce. Research on Lanyu scops owls (*Otus elegans botelensis*) points in this direction. It was found that site fidelity was related to breeding success, and mate fidelity was related to female site fidelity and pair duration (Bai & Severinghaus, 2012). This made it impossible to subscribe the results of this study to either the incompatibility hypothesis or the better option hypothesis. On the contrary, the opposite was found in *Procellariiformes* (albatrosses and petrels). Bried *et al*. (2002) revealed that in the *Procellariiformes* mate fidelity was not related to site fidelity. There was high mate fidelity but low nest fidelity.

This makes a conclusion on the causes of divorce in long-term monogamous birds all the more difficult. When taking all into account, I find it is most likely that it cannot be said that divorce has one clear cause. It is likely that the process of divorce varies between and within species and populations. Personally, based on previous chapters, I think that there is only one cause for divorce: when there is a possibility to improve reproductive success, divorce will take place. Whether this is due to incompatibility or a possible better mate, accidental loss or forced divorce, I do not know. However, I suggest that this makes no difference for the cause of divorce, since in the end, all these hypotheses eventually result in an improved reproductive success (even when considering the accidental loss hypothesis, reproductive success will be increased by divorce since waiting for a

partner to return may have such high costs that it would disenable the pair members to breed in that specific year). So far, no clear contradictions to this contemplation have been found in the literature used for this literature study. Still, one should always remember that these contemplations are mostly based on correlations. It would be best to have some experimental, non-laboratory research on the causes (as earlier described in this discussion) on divorce before drawing any final conclusions.

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