

Article

Fitness consequences of divorce in the azure-winged magpie depends on the breeding experience of a new mate

Li-Fang GAO, Hai-Yang ZHANG, Wen ZHANG, Xiao-Dan ZHANG, Zhen-Qin ZHU, and Bo DU*

School of Life Sciences, Lanzhou University, Tianshui South Road 222#, Lanzhou City, Gansu Province, 730000, China

*Address correspondence to Bo Du. E-mail: dubo@lzu.edu.cn

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Abstract

Sexual conflict in producing and raising offspring is a critical issue in evolutionary ecology research. Individual experience affects their breeding performance, as measured by such traits of provisioning of offspring and engagement in extra-pair copulations, and may cause an imbalance in sexual conflict. Thus, divorce is hypothesized to occur within aged social pairs, irrespective of current reproductive success. This concept was explored in the azure-winged magpie *Cyanopica cyanus* by investigating the divorce of a social pair and its relationship to their changes in breeding performance with prior experience. Females engaging in extra-pair copulation may intensify sexual conflicts and may be the main reason for divorce. Once divorced, females repairing with an inexperienced male realized higher reproductive success than that repairing with an experienced male; males repairing with an experienced female realized higher reproductive success than that repairing with an inexperienced female. This finding indicates that the fitness consequence of divorce depends on the breeding experience of new mates. Divorced females can obtain more extra-pair copulations, whereas divorced males cannot, when they repair with inexperienced breeders. Divorced females provisioned a brood at lower rates than inexperienced females whereas divorced males had no such difference. It appears that divorced females can obtain an advantage in sexual conflicts with inexperienced mates in future reproduction. Consequently, females are probably more active than males in divorcing their aged mates so as to select an inexperienced male as a new mate. Azure-winged magpies thus provide novel insights into the implications of sexual conflict in birds.

Key words: breeding experience, extra-pair copulation, parental care, provisioning rate, sexual conflict

In gamogenetic animals, males and females differ in their approaches to maximize individual fitness, with males often focused on producing offspring and females investing more in raising offspring (Bateman 1948; although many exceptions to this general tenet are acknowledged). Hence, sexual conflicts between paired males and females occur through both producing and raising

offspring (Andersson 1994; Lessells 2012). The sex that can acquire a dominant position in sexual conflicts often over-exploits the parental effort of its social mate, for example, females that engage in extra-pair copulations (Griffith et al. 2002). The exploited sex will be driven to make adaptive responses, among which is 1 divorce (Smith 1984). Empirical studies have uncovered that divorce is

widespread in birds (Choudhury 1995) and that divorce rates vary greatly among species (Ens et al. 1996). The fitness consequences and the reasons for divorce can be quite variable.

Current hypotheses suggest that the reasons for divorce determine their fitness consequences. In cases in which a social pair have lower reproductive success than expected, due to incompatibility or initial errors in mate selection, the costs of maintaining pair fidelity will outweigh its benefits (Johnston and Ryder 1987; Triefenbach and Itzkowitz 1998). As a result, both sides might initiate the divorce and are expected to enhance reproductive success in remating with new partners (Ens et al. 1993; Moody et al. 2005). In other cases, if 1 partner of a social pair is ousted by a stronger competitor (Jeschke et al. 2007; Maness and Anderson 2008) or if it loses a territory because of late arrival, the other partner might repair (Dhondt and Adriaensen 1994; García-Navas and Sanz 2011). Under such circumstances, divorce becomes a by-product of outside factors; and divorced individuals do not necessarily enhance reproductive success in their after-divorce reproduction. Therefore, to determine whether the divorce has a positive or negative consequence to individual fitness, it is essential to identify the factors that might drive a social pair to divorce (Dhondt 2002).

Breeding performance of individuals, indexed by parental effort in raising offspring and engagement in extra-pair copulations, may influence the decision of divorce for a social pair, particularly because it often varies with the breeding experience of individuals (Saether 1990; Martin 1995). On the one hand, experienced breeders have higher resource-holding potential due to accumulated breeding skills (Blas et al. 2009; Zabala and Zuberogaitia 2015) or enhanced capacity because they have access to high-quality resources (Daunt et al. 2007; Martínez et al. 2008). Therefore, they are expected to provide more parental care for offspring than their inexperienced counterparts and hence have reduced conflicts with their mates over parental care. On the other hand, older breeders often engage in a higher level of extra-pair copulations than younger breeders (Richardson and Burke 1999; Dickinson 2001; Bouwman et al. 2007); they are expected to intensify conflicts with their mates over paternity. The antagonistic effects of experience on individual breeding performance influence not only the tradeoff of paired individuals between maintaining the intact pairing and divorcing their aging partner (Ramsay et al. 2000; Naves et al. 2006), but also that of unpaired individuals between selecting an older, experienced breeder and a younger, inexperienced breeder as their social mate (Dhondt 2002). Because older, experienced breeders cope with breeding conditions better (Hatchwell et al. 1999; Martínez et al. 2008) and can better compete with inexperienced breeders (Jaatinen and Öst 2011), they are more likely to gain an edge in sexual conflicts if they pair with inexperienced breeders. That is, they provide less parental care in raising offspring (i.e., making their social mates contribute more to raising offspring) and/or engage in more extra-pair copulations (or prevent their social mates from engaging in extra-pair copulations). Consequently, when the experience-related change of individual breeding performance causes an imbalance in sexual conflicts of aged pairs, it may drive a social pair to divorce and repair with a younger breeder irrespective of current reproductive success.

We tested the effect of experience-related change in breeding performance on the divorce of animals in the azure-winged magpie *Cyanopica cyanus*. It is a cooperatively-breeding bird that breeds on the Tibetan Plateau in a high-density nesting pattern (20–180 nests/ha, Ren et al. 2016). Nest predation and conspecific nest-raiding are the main reasons for nest failure; accordingly, helpers in cooperative

groups contribute more to nest defense than to brood provisioning (Ren et al. 2016). Parentage analyses in this Tibetan population found a high level of extra-pair fertilizations that included both extra-pair paternity (EPP) and maternity (EPM, Gao et al. 2018). In such a community, EPP-cuckolded males and EPM-cuckolded females raise unrelated young whereas EPM-cuckolded males and EPP-cuckolded females raise only their offspring. Interestingly, a study of parental provisioning behaviors revealed that cuckolded breeders of the Tibetan azure-winged magpie increased parental efforts in a nest with their offspring but did not reduce parental efforts in nests containing extra-pair young (EPY; Gao et al. 2019). These results indicate that sexual conflicts in social pairs of azure-winged magpies are remarkably intense, not only over parentage but also over parental care. In this context, the relationship between experience-related changes of individual breeding performance and divorce becomes a question central to understanding the evolution ecology of Tibetan azure-winged magpie.

In this study, we addressed 1) whether the reproductive success and breeding performance of both sexes in the current pair were correlated with the likelihood of the pair to divorce by the subsequent breeding season; 2) whether reproductive success differed between before- and after-divorce breeding of divorced individuals, as well as among social pairs formed by different-experience breeders; and 3) whether the engagement in extra-pair copulations and provisioning of offspring differed between experienced and inexperienced breeders.

Methods

Study area and population

This study was performed in the northeast of the Tibetan Plateau (102.5°E, 34.6°N, height 3,400 m) from 2011 to 2019. The climate of the region is characterized by low temperature (2.3°C) and high precipitation (annual average of 782 mm). The typical landscape is an alpine meadow, with shrubs composed mainly of *Berberis hemisleyana* and *Hippophae rhamnoides*. Azure-winged magpies prefer to build nests on *H. rhamnoides* and *Salix caprea* in a highly-clumped pattern. In a previous study, the breeding density ranged between 20 and 180 nests/ha (Ren et al. 2016). The breeding season lasts from late April to mid-September, including ~1 month of the postfledging period. In mid-April, azure-winged magpies begin migrating from their wintering site (in a spruce forest at a lower altitude of 2,200 m) to their breeding site. Experienced breeders usually arrive at or in the vicinity of their previous territory.

Adult banding and identification

We began to capture and band this population in 2011. Adult birds were captured by mist net at the end of April or by scalable loops when they provisioned the broods (Ren et al. 2016). The capture was performed after the Wildlife Conservation Law of the 10th National People's Congress of China (28 August 2004). It caused no known harmful effect to the birds as evidenced by the fact that no nest abandoning occurred due to capture. Each adult was leg-banded with a numbered aluminum band and a unique combination of 2 plastic colored rings. The birds' body mass was weighed to the nearest 0.1 g and their tarsus length was measured to the nearest 0.1 mm. About 20 μ L of blood was sampled from the brachial vein of each bird, treated with 4% EDTA in physiological saline as anti-coagulant, and then stored in absolute ethyl alcohol.

Age of breeders that were banded when they were chicks could be precisely determined. They were termed age 1. Breeders without

rings and those banded when they were adults were labeled as “age unknown.” The mating status of a breeder was determined according to its leg rings. An individual in its first breeding attempt was labeled as an “inexperienced breeder” and individuals in their second or later breeding attempt were labeled as “experienced breeder.” If both sides of a social pair were experienced and reunited, they were labeled as “intact-pairing.” If both sides were experienced but repaired with a new partner they were labeled as “divorced.” If only 1 side was recaptured, it was labeled as “mating status unknown.” According to the leg rings of both sexes, the types of social pairs were identified and included “inexperienced female/male,” “inexperienced female/divorced male,” “divorced female/inexperienced male,” and “experienced female/male”—a category that included “divorced female/male” and “intact pairs.” In this study area, azure-winged magpies brood once a year, so divorce occurs across breeding seasons. Only individuals identified between 2013 and 2018 were used in subsequent analyses because their mating status and whether they had divorced could be determined. Individuals with unknown age or mating status were excluded from the analyses.

Life-history data collection

During the egg-laying period, nest contents were checked daily to ascertain the clutch initiation date and size. For individual identification, on the hatching day, each hatchling was marked on its abdomen according to its hatching sequence, using a nontoxic marking pen; its body mass was then weighed to the nearest 0.1 g. Thereafter, the hatchlings’ body mass was measured every 2 days. When chicks reached 40 g, we leg-banded and blood-sampled them using the same method as in adults. Any missing egg or chick was recorded as offspring loss.

Adult provisioning rates were recorded by digital camcorders (ZX1; Eastman Kodak Company). The camcorders were positioned on tripods, fixed 1 m diagonally above the nest during nest construction. This procedure minimized disturbance to the adults with no nest abandoning having occurred because of the presence of the tripod and camcorder. Recordings were performed every 2 days between 09:00 and 12:00. A total of 1,400 h of provisioning behaviors of adults in 250 nests (mean \pm standard errors [SEs], 5.6 ± 0.1 h) were recorded. Data on the number of feeding bouts per hour were extracted from the video recordings and the identity of provisioner was determined based on the leg bands.

Parentage analysis

Genomic DeoxyriboNucleic Acid (DNA) was extracted from blood samples using a genomic DNA kit (Tiangen Biotech Co., Beijing, China). Ten primer pairs of polymorphic microsatellites were used to perform genotyping (Supplementary Appendix I, Gao et al. 2018). A polymerase chain reaction (PCR) system of 10 μ L was composed of 1 \times buffer, 1.5 mM MgCl₂, 100 nM of each primer, 200 nM of each deoxy-ribonucleoside triphosphate (dNTP), 0.5 U of Taq DNA polymerase, and 100 pg genomic DNA as the template. The PCR program started with a predenaturation step at 94°C for 5 min, which was then followed by 35 cycles of 95°C for 30 s, 47.5–59°C (Gao et al. 2018) for 30 s, and 72°C for 30 s. The program ended with a final extension step at 72°C for 5 min. About 2 μ L of the PCR product was separated on 6% polyacrylamide gel and bands were then silver-stained. DNA profiles were inspected to identify putative alleles, based on which the genotype of each was scored. Cervus was used to perform parentage analysis (Kalinowski

et al. 2007). We first used parentage exclusion to identify EPY in each nest, then we used the parentage assignment to identify the genetic parents of each EPY with all sampled adults as candidates. The confidence level was 95% for parentage exclusion and 80% for parentage assignment. An individual that produced EPY was considered as engaging in cuckoldry.

Statistical analysis

To examine factors that might correlate with whether a social pair divorced after mating once, a generalized linear model was fitted, with predictor variables including current fecundity (clutch size in the current breeding), percentage of offspring that fledged successfully, male’s contribution to brood provisioning, whether the male and female engaged in extra-pair copulations and social pair types (Table 1). Generalized linear mixed models (GLMMs) were then fitted to examine factors correlated with whether a breeder engaged in extra-pair copulations. Fixed effects included clutch initiation date, the tarsus length and age of the breeders, and social pair types. Random effects included the year and identity of the breeder. Another GLMM was fitted to examine factors correlated with male’s contribution to brood provisioning, in which fixed effects included whether the female engaged in extra-pair copulations, the tarsus length and age of both breeders, and social pair types. Random effects included the year, nest identity, and identity of both breeders.

Fecundity, the number and body mass of fledglings (averaging the offspring of 1 nest) of experienced breeders, was compared between before- and after-divorce breeding, using a paired-sample *t*-test. The fecundity, the number, and body mass of fledglings (averaging the offspring of 1 nest) of different social pair types were compared using 1-way ANOVA analysis.

All analyses were carried out using SPSS for Windows (version 19.0; IBM, Armonk, NY, USA). Descriptive results are presented as mean \pm SEM. The null hypotheses were rejected when $P < 0.05$. Probabilities are reported as 2-tailed.

Data accessibility

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bk3j9kd70>.

Results

Based on the mark-recapture data, the breeding experience of both sexes could be determined in 307 azure-winged magpie nests in which clutches completed. Of these, 68% (208/307) successfully fledged at least 1 offspring. Recruitment rates of female and male inexperienced breeders were $55\% \pm 15\%$ and $62\% \pm 13\%$ (for 6 years of data), respectively. The annual divorce rate of the Tibetan azure-winged magpie was $72\% \pm 5\%$.

Factors correlated with the divorce of a social pair

The likelihood of divorce of a social pair by subsequent breeding season was unrelated to their current fecundity, percentage of offspring that failed to fledge, and male’s contribution to brood provisioning (Table 1). A social pair more likely divorced when the female engaged in extra-pair copulations than when she did not. In contrast, a social pair less likely divorced when the male engaged in extra-pair copulations than when he did not (Table 1). Compared with pairs formed by inexperienced females and males, pairs formed by 2 experienced breeders had a lower likelihood of divorce and

Table 1. Factors correlated with whether a social pair divorced by the subsequent breeding season

Parameters	$\beta \pm SE$	<i>n</i>	X_1^2	<i>P</i> -value
Intercept	1.36 ± 2.48	105	0.30	0.58
Current fecundity (clutch size in the current breeding season)	0.41 ± 0.29	105	1.98	0.16
Percentage of offspring that fledged successfully	0.11 ± 0.88	105	0.02	0.90
Males' contribution to brood provisioning	-3.20 ± 2.08	105	2.37	0.12
^a Whether female engaged in extra-pair copulations	1.62 ± 0.68	105	5.72	0.02
^b Whether male engaged in extra-pair copulations	-1.30 ± 0.58	105	-5.07	0.02
^c Pairing patterns				
Inexperienced female, experienced male	-0.52 ± 1.05	12	0.25	0.62
Experienced female, inexperienced male	0.3 ± 0.98	15	0.15	0.70
Experienced female, experienced male	-2.6 ± 0.84	18	9.76	0.002

Variables in bold font indicate statistical significance ($P < 0.05$).

^aFemales engaging in no extra-pair copulations were set as zero.

^bMales engaging in no extra-pair copulations were set as zero.

^cPairs formed by inexperienced female and male ($n = 60$) were set as zero.

pairs of mixed inexperienced and experienced breeders exhibited no significant differences (Table 1).

Reproductive success comparison of experienced breeders

Fecundity of experienced breeders did not differ significantly between their inexperienced and subsequently experienced reproduction (Figure 1A, Supplementary Appendix I). The fecundity of divorced males that had repaired with inexperienced females was significantly lower in their after-divorce breeding when compared with that in their before-divorce breeding (Figure 1A, Supplementary Appendix I). In terms of fledgling numbers, experienced breeders did not increase their reproductive success, regardless of pair composition (Figure 1B, Supplementary Appendix I). Divorced males that had repaired with inexperienced females raised fewer fledglings than the number before the divorce (Figure 1B, Supplementary Appendix I).

Intact pairs fledged significantly larger offspring in their experienced reproduction than in their inexperienced reproduction (Figure 1C, Supplementary Appendix I). Similarly, divorced males that had repaired with inexperienced females raised significantly larger offspring in their after-divorce breeding than in their before-divorce breeding (Figure 1C, Supplementary Appendix I). The divorced female that had repaired with inexperienced males exhibited no difference in fledgling body mass between their before- and after-divorce breeding (Figure 1C, Supplementary Appendix I). For divorced females or males that had repaired with a divorced breeder, the offspring they fledged were significantly smaller than those they fledged before the divorce (Figure 1C, Supplementary Appendix I).

Comparison of reproductive success of different social pairs

The fecundity of different social pairs differed significantly (Figure 2A, Supplementary Appendix II). Experienced females, either divorced or within intact pairs, had higher fecundity than inexperienced females (Figure 2A). Inexperienced females that had paired with a divorced male had the lowest fecundity (Figure 2A). In terms of fledgling number, intact pairs fledged the most offspring whereas divorced males that repaired with inexperienced females fledged the fewest offspring (Figure 2B, Supplementary Appendix II). Fledgling body mass was the highest in intact pairs whereas it was the lowest when divorced males had repaired with inexperienced females (Figure 2B, Supplementary Appendix II).

Individual breeding performance in terms of engaging in extra-pair copulations

The likelihood that a female engaged in extra-pair copulations significantly increased with clutch initiation date and decreased with the age of its social mate, but it did not change with the tarsus length or age of the female (Table 2). Later breeding initiation made females more likely to engage in extra-pair copulations and pairing with older males made females less likely to engage in extra-pair copulations. Females in different pair types differed in their likelihood of engaging in extra-pair copulations (Table 2). Between-year differences contributed to the variance of females engaging in extra-pair copulations were greater than that between individuals (Table 2). Divorced females repairing with inexperienced males engaged in extra-pair copulations more than those repairing with divorced males or their original mates (Figure 3).

The likelihood that a male engaged in extra-pair copulations did not change with the tarsus length or age of either sex, but it tended to increase with clutch initiation date ($P = 0.08$; Table 2). Males were more likely to engage in extra-pair copulations when breeding initiation was late. Males in different pair types differed significantly in their likelihood of engaging in extra-pair copulations (Table 2). Between-year differences contributed to the variance of males engaging in extra-pair copulations were greater than that between individuals (Table 2). Divorced males repairing with inexperienced females engaged in extra-pair copulations more than those repairing with divorced females but less than those repairing with their original mates (Figure 3).

Individual breeding performance in terms of contribution to brood provisioning

Males' contribution to brood provisioning did not change with their tarsus length or the age of either sex; however, it differed significantly between males whose partners engaged or not in extra-pair copulations and tended to differ among different pairing patterns (Table 3). Between-year differences contributed to the variance of males' contribution to brood provisioning and were greater than that between nests and individuals (Table 3). Males made a significantly lower contribution to brood provisioning when their partners engaged in extra-pair copulations than when they did not (Figure 4A). Divorced males made a similar contribution to brood provisioning to inexperienced males either when they repaired with a divorced or inexperienced female (Figure 4B). Divorced females contributed less to brood provisioning than inexperienced females either when they repaired with a divorced or inexperienced male (Figure 4B).

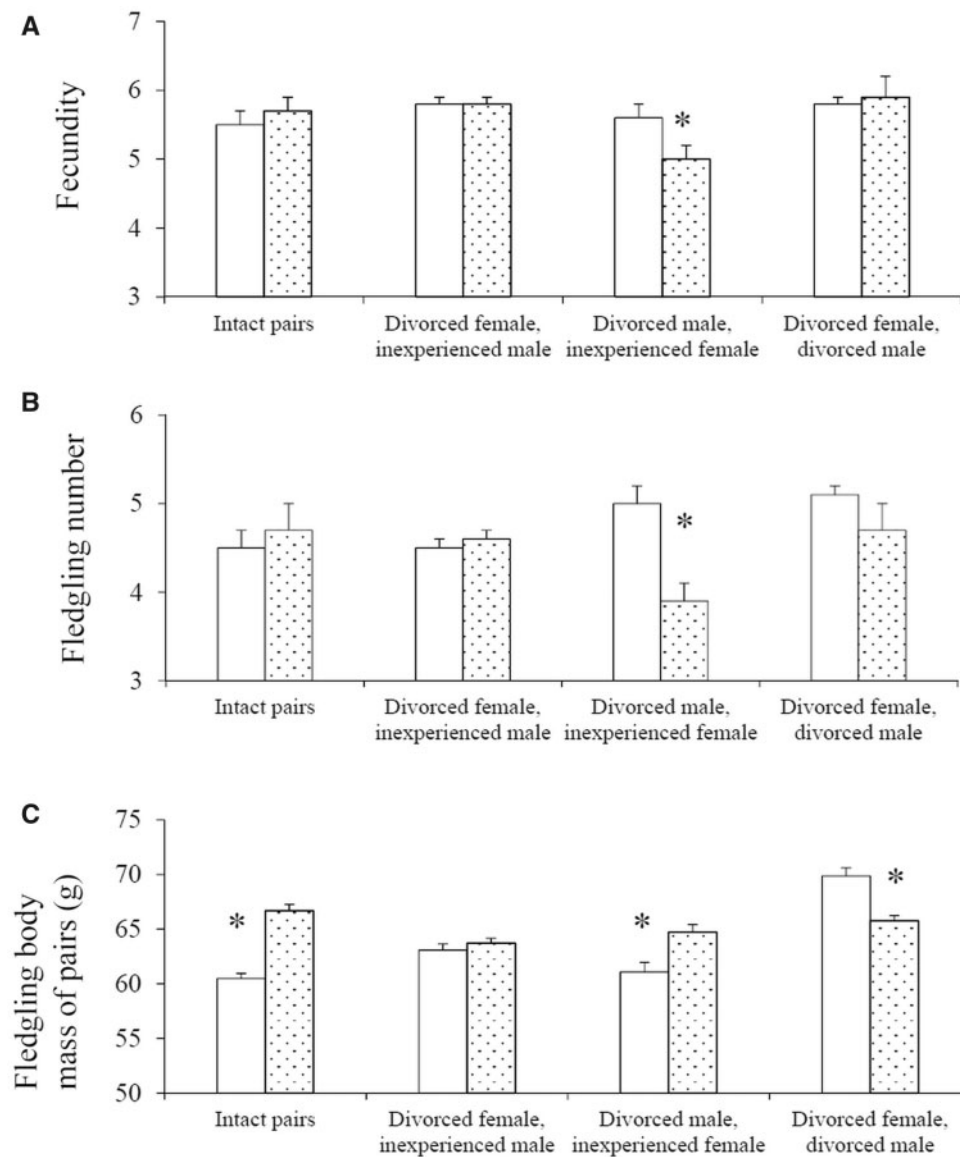


Figure 1. Comparison of fecundity (A), fledgling number (B), and body mass (C) of experienced breeders during breeding before (blank columns) and after (filled columns) divorce. Bars are SEs, and asterisks indicate experienced breeders that differ ($P < 0.05$) in their breeding traits between inexperienced and subsequent experienced breeding.

Discussion

In Tibetan azure-winged magpies, females engaging in extra-pair copulations seem to significantly affect the likelihood of divorce of a social pair. Compared with maintaining an intact pairing, divorced individuals of both sexes do not necessarily increase their after-divorce reproductive success. The breeding experience of a new mate determines whether a divorced individual could obtain positive lifetime fitness benefits from the divorce.

Female engagement in extra-pair copulations, which will intensify sexual conflicts over paternity and parental care, may be the main reason for divorce in the azure-winged magpie. Cuckoldry of females usually results in paternity loss of cuckolded males (Andersson 2001; Arnold and Owens 2002), whereas cuckoldry of males rarely reduces the fertilization of affected females (Dixon et al. 1994; Suter et al. 2009). Female engagement in extra-pair copulations will cause paternity loss of cuckolded males, but not vice

versa. Consequently, females' engagement in extra-pair copulations, but not that of males, is more likely to increase the probability of divorce (Table 1). As a "retaliation" response to the cuckoldry of social mates, the divorce strategy adopted by cuckolded individuals occurs more frequently after a reproductive period than during it (Cezilly and Nager 1995). The reason is that if cuckolded individuals abandon the mixed brood during current reproduction, they might endure the costs of wasting their invested energy without any reward (Gao et al. 2018). In the azure-winged magpie, cuckolded males increase, or at least maintain care for a mixed brood (Gao et al. 2018, 2019). It thus increases the likelihood that their offspring fledge successfully. Consequently, azure-winged magpies are likely to divorce their cuckolded mates after the reproductive period. Moreover, both sexes have raised their nestlings by adopting a brood survival strategy (Da et al. 2018). Therefore, nest failure in the Tibetan azure-winged magpies should be attributed mainly to

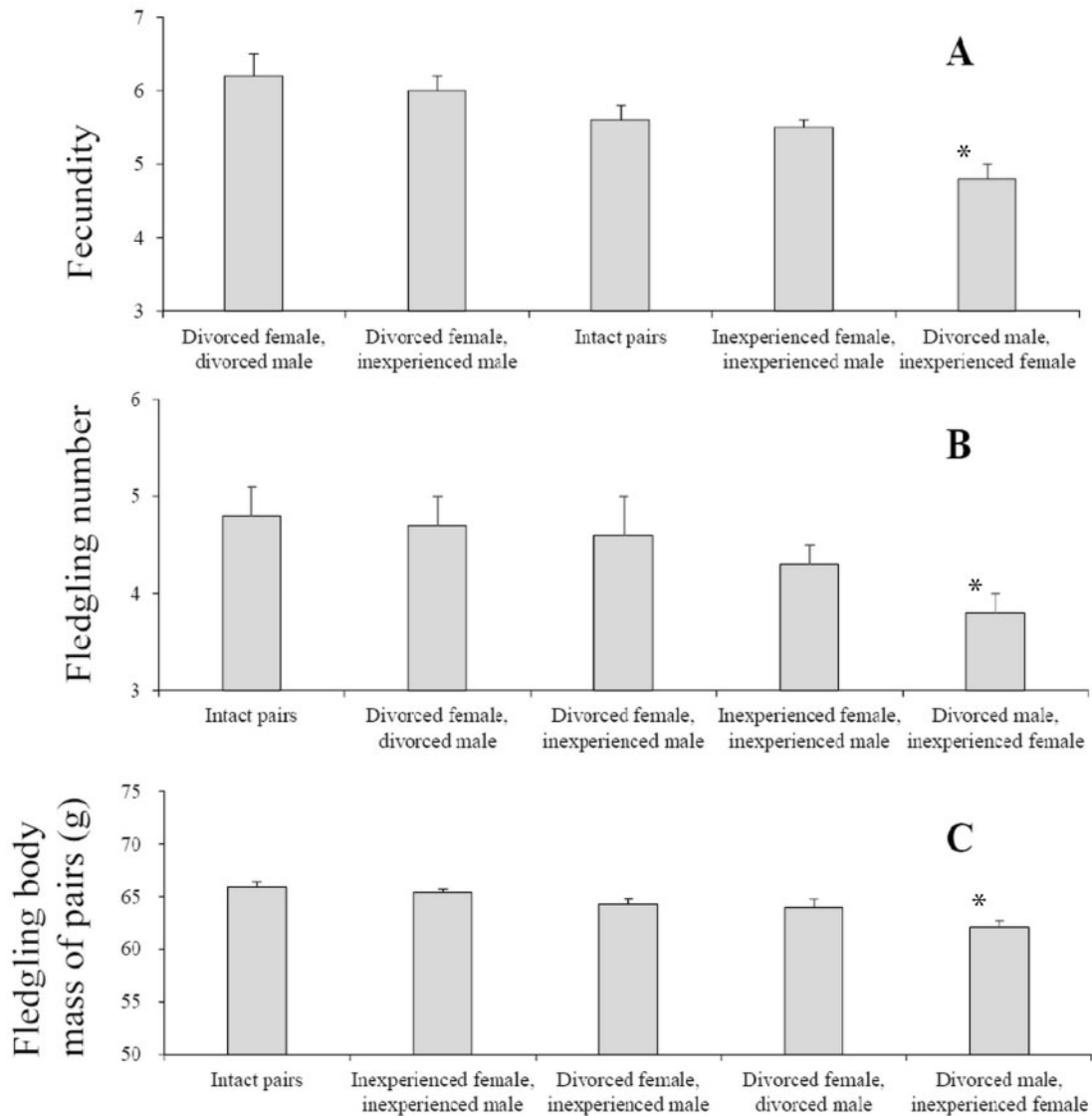


Figure 2. Comparison between social pair types in terms of fecundity (A), fledgling number (B), and body mass (C). Bars are SEs, and asterisks indicate that different social pair types differ ($P < 0.05$) significantly in their breeding traits.

natural predators or conspecific nest-raiders (Ren et al. 2016), but not to breeders. This explains why the divorce of the Tibetan azure-winged magpies is unrelated to the fecundity and reproductive success in current reproduction.

In terms of reproductive success, whether an individual gains positive consequence from divorce depends largely on the breeding experience of their new mate. Most studies have reported that the causes of divorce are the major determinants of their fitness consequences, with the proactive side in divorce more likely having a positive consequence in their after-divorce breeding (Moody et al. 2005; Naves et al. 2006; Ludwigs and Becker 2007; Maness and Anderson 2008; Valcu and Kempenaers 2008). However, we find in the azure-winged magpie that the breeding experience of new mates determines the fitness consequence of divorce in both sexes. For divorced females, when they repair with experienced males, their after-divorce reproductive success decreases significantly compared with that in their before-divorce breeding (Figure 1); their after-divorce reproductive success exhibits no difference between remating with

experienced and inexperienced males (Figure 2). For divorced males, when they repair with inexperienced females, they fledge fewer but larger offspring in their after-divorce breeding than before-divorce breeding (Figure 1); they fledge fewer and smaller offspring when remating with inexperienced females than with experienced females (Figure 2). Therefore, from the viewpoint of fitness consequences, it will be more beneficial for divorced females to repair with inexperienced males and divorced males to repair with experienced females.

The experience-related changes of individual breeding performance, which affect the intensity of sexual conflicts, will result in a sex-based difference between experienced breeders in selecting their new mates, and, in turn, determine which sex more likely becomes the initiator of divorce. Because engagement in extra-pair copulations and potential of brood provisioning both increase with age (Sundberg and Dixon 1996; Bouwman et al. 2007; Blas et al. 2009; Zabala and Zuberogoitia 2015), their antagonistic effects will influence the mate selection of individual breeders (Iwasa and Harada 1998), including divorced individuals in selecting their new partners.

Table 2. Factors correlated with whether the female or male engaged in extra-pair copulations, as examined by fitting GLMMs

Parameters of the GLMM	Female			Male		
	<i>F</i>	df1, df2	<i>P</i> -value	<i>F</i>	df1, df2	<i>P</i> -value
Clutch initiation date	3.91	1,332	0.05	3.14	1,317	0.08
Tarsus length of the breeder	1.24	1,332	0.27	0.37	1,317	0.55
Female age	0.09	1,332	0.76	2.30	1,317	0.13
Male age	5.43	1,332	0.02	0.03	1,317	0.86
Social pair types	2.12	4,332	0.08	3.54	4,317	0.008
Random effects	Variance ± SD		VCA	Variance ± SD		VCA
Year	0.2067 ± 0.4547		0.62	0.2865 ± 0.5352		0.83
Identity of the breeder	0.0841 ± 0.2899		0.25	0.0286 ± 0.1692		0.08
Residual	0.0447 ± 0.2115		0.13	0.0290 ± 0.1702		0.09

The year and the identity of female or male were set as random effects. VCA is the variance component analysis for random effect variables. Variables in bold font indicate statistical significance ($P < 0.05$).

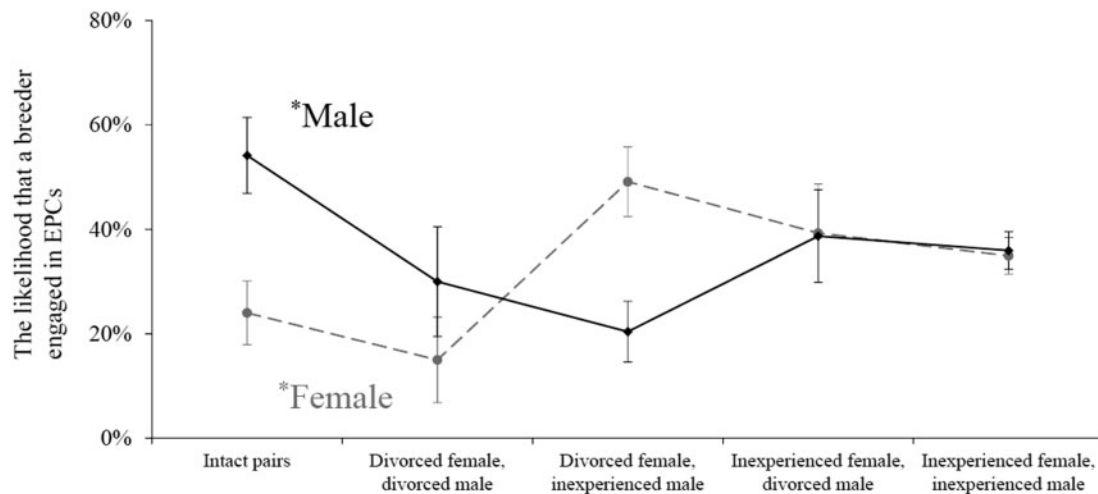


Figure 3. The likelihood of a female (circles) and male (diamonds) engaging in extra-pair copulations in different social pair types. Bars are SEs obtained in fitting the GLMMs. Asterisks indicate that the likelihood of a breeder engaged in extra-pair copulations differed significantly ($P < 0.05$) among different social pair types.

Table 3. Factors correlated with males' contribution to brood provisioning, examined by fitting GLMMs

Parameters	<i>F</i>	df1, df2	<i>P</i> -value
Fixed effects			
Whether the female engaged in extra-pair copulations	5.63	1,317	0.02
Tarsus length of the breeder	0.45	1,317	0.50
Female age	2.78	1,317	0.10
Male age	1.25	1,317	0.26
Social pair types	1.99	4,317	0.07
Random effects	Variance ± SD		VCA
Year	0.0113 ± 0.1063		0.22
Nest identity	0.0042 ± 0.0605		0.08
Female identity	0.0001 ± 0.00006		0.0002
Male identity	0.00001 ± 0.00001		0.0002
Residual	0.0367 ± 0.192		0.70

The year, the identity of the nest, and identity of both sexes were set as random effects. Variables in bold font indicate statistical significance ($P < 0.05$).

In the azure-winged magpie, sexual conflicts might be intensified mainly by females' performance in the engagement in extra-pair copulations (Table 1), but also by males' performance in brood provisioning because males contribute to raising offspring significantly greater than females (Ren et al. 2016). These 2 aspects cause different sexual conflicts among different types of social pairs (Figures 3 and 4). Within social pairs formed by an experienced female and male, either an intact pairing or both divorced, females engage in extra-pair copulations at a lower frequency (Figure 3) and males make a greater contribution to brood provisioning (Figure 4B). Thus, sexual conflicts in these 2 types of pairs would be low, explaining why they realize higher reproductive success than in other pairs (Figure 2). When divorced females repair with inexperienced males, they engage in extra-pair copulations at the highest frequency (Figure 3) and their mates make the greatest contribution to brood provisioning (Figure 4B). It seems that the experienced females in such pairs are in control of the sexual conflicts, hence, their final reproductive success does not differ from that of intact pairs (Figure 2). When divorced males repair with inexperienced females, their social mates engage in extra-pair copulations at a

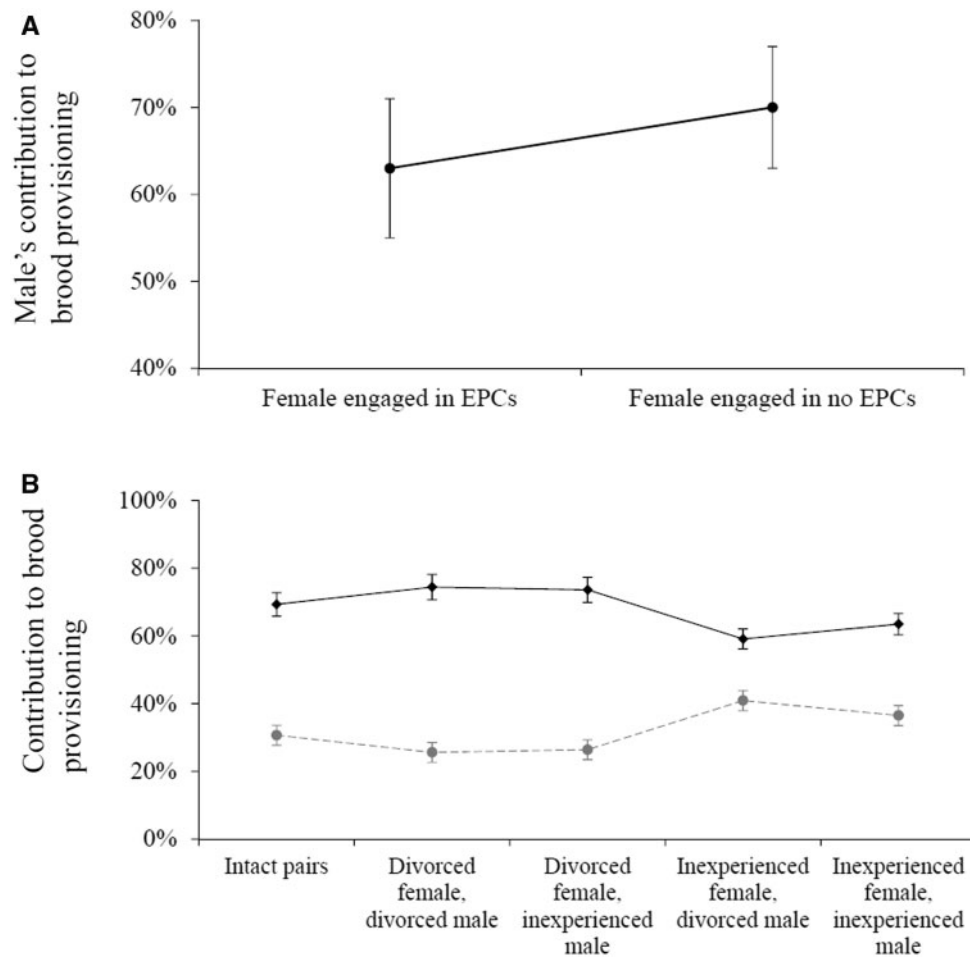


Figure 4. Males' relative contribution to brood provisioning as a factor of their female partners being engaged or not in extra-pair copulations (**A**), and males' (diamonds) and females' (circles) relative contribution to brood provisioning in different social pair types (**B**). Bars are SEs obtained in fitting the GLMM.

higher frequency (Figure 3) and they make the lowest contribution to brood provisioning (Figure 4B). These pairs might have the highest sexual conflict, which could explain why they achieve the lowest reproductive success of all pair types (Figure 2). Consequently, in terms of potential dominance in future sexual conflicts, it will be more beneficial for experienced females to repair with inexperienced males and experienced males to repair with experienced females. This sexual difference of experienced breeders in selecting between experienced and inexperienced breeders determines which sex more likely initiates the divorce. As there is a high recruitment rate of inexperienced breeders in the Tibetan population, it would appear easy for experienced females to select an inexperienced male as new mate and then obtain an advantage in the sexual conflict (more extra-pair copulation chances, Figure 3; fewer efforts in raising offspring, Figure 4B). In contrast, it would be difficult for experienced males to repair with an experienced female because the latter prefers to repair with inexperienced males. Therefore, females are more likely the initiator of divorce.

Our study reveals that divorce in the Tibetan azure-winged magpies does not necessarily result in positive consequences to individual fitness in a single breeding season. However, as experienced breeders gain an advantage in sexual conflicts by divorcing their aged partners and then selecting new mates, divorce may be beneficial for individuals to realize higher life-time reproductive success. As an alternative breeding strategy, the effect of divorce on

individual life-time fitness warrants further investigation in future studies. Such model systems provide key insights into the complex dynamics of the evolutionary ecology of bird species.

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Conflict of Interest

All authors have no conflicts of interest to any other institutions.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

References

- Andersson M, 1994. *Sexual Selection*. Princeton (NJ): Princeton University Press.
- Andersson M, 2001. Relatedness and the evolution of conspecific brood parasitism. *Am Nat* 158:599–614.
- Arnold KE, Owens IPF, 2002. Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation. *Proc Biol Sci* 269:1263–1269.
- Bateman AJ, 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
- Blas J, Sergio F, Hiraldo F, 2009. Age-related improvement in reproductive performance in a long-lived raptor: a cross-sectional and longitudinal study. *Ecography* 32:647–657.
- Bouwman KM, Van RE, Vijmenga DJ, Komdeur J, 2007. Older male reed buntings are more successful at gaining extrapair fertilizations. *Anim Behav* 73:15–27.
- Cezilly F, Nager R, 1995. Comparative evidence for a positive association between divorce and extra-pair paternity in birds. *Proc Biol Sci* 262:7–12.
- Choudhury S, 1995. Divorce in birds: a review of the hypotheses. *Anim Behav* 50:413–429.
- Da XW, Xian LL, Luo JJ, Gao LF, Du B, 2018. Azure-winged Magpies *Cyanopica cyanus* trade off reproductive success and parental care by establishing a size hierarchy among nestlings. *IBIS* 160:769–778.
- Daunt F, Wanless S, Harris MP, Money L, Monaghan P, 2007. Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. *Funct Ecol* 21:561–567.
- Dhondt AA, Adriaensen F, 1994. Causes and effects of divorce in the blue tit *Parus caeruleus*. *J Anim Ecol* 63:979–987.
- Dhondt AA, 2002. Changing mates. *Trends Ecol Evol* 17:55–56.
- Dickinson JL, 2001. Extrapair copulations in western bluebirds (*Sialia mexicana*): female receptivity favors older males. *Behav Ecol Sociobiol* 50:423–429.
- Dixon A, Ross D, O'Malley SLC, Burke T, 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature* 371:698–700.
- Ens BJ, Choudhury S, Black JM, 1996. Mate fidelity and divorce in monogamous birds. In: Black JM, editor. *Partnerships in Birds: The Study of Monogamy*. Oxford: Oxford University Press. 344–395.
- Ens BJ, Safriel UN, Harris MP, 1993. Divorce in the long-lived and monogamous oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? *Anim Behav* 45:1199–1217.
- Gao LF, Xian LL, Luo JJ, Du B, 2018. High level of extrapair fertilization in individual Tibetan azure-winged magpies and their adaptive responses. *J Avian Biol* 2018:e01739.
- Gao LF, Zhang HY, Zhan W, Sun YH, Liang MJ et al., 2019. Effects of extra-pair paternity and maternity on the provisioning strategies of the azure-winged magpie *Cyanopica cyanus*. *IBIS*. (In press). doi: 10.1111/ibi.12800.
- García-Navas V, Sanz JJ, 2011. Females call the shots: breeding dispersal and divorce in blue tits. *Behav Ecol* 22:932–939.
- Griffith SC, Owens IPF, Thuman KA, 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol Ecol* 11:2195–2212.
- Hatchwell BJ, Russell AF, Fowlie MK, Ross DJ, 1999. Reproductive success and nest-site selection in a cooperative breeder: effects of experience and a direct benefit of helping. *Auk* 116:355–363.
- Iwasa Y, Harada Y, 1998. Female mate preference to maximize paternal care. II. Female competition leads to monogamy. *Am Nat* 151:367–382.
- Jaatinen K, Öst M, 2011. Experience attracts: the role of age in the formation of cooperative brood-rearing coalitions in eiders. *Anim Behav* 81:1289–1294.
- Jeschke JM, Wanless S, Harris MP, Kokko H, 2007. How partnerships end in guillemots *Uria aalge*: chance events, adaptive change, or forced divorce? *Behav Ecol* 18:460–466.
- Johnston VH, Ryder JP, 1987. Divorce in larids: a review. *Colon Waterbird* 10:16–26.
- Kalinowski ST, Taper ML, Marshall TC, 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol* 16:1099–1106.
- Lessells CM, 2012. Sexual Conflict. In: Royle NJ, Smiseth PT, Kölliker M, editors. *The Evolution of Parental Care*. Oxford: Oxford University Press. 150–170.
- Ludwigs JD, Becker PH, 2007. Is divorce in young common terns, *Sterna hirundo*, after recruitment just a question of timing? *Ethology* 113:46–56.
- Maness TJ, Anderson DJ, 2008. Mate rotation by female choice and coercive divorce in Nazca boobies, *Sula granti*. *Anim Behav* 76:1267–1277.
- Martin K, 1995. Patterns and mechanisms for age-dependent reproductive and survival in birds. *Am Zool* 35:340–348.
- Martínez JA, Calvo JF, Martínez JE, Zuberogoitia I, Zabala J et al., 2008. Breeding performance, age effects and territory occupancy in a Bonelli's eagle *Hieraetus fasciatus* population. *IBIS* 150:223–233.
- Moody AT, Wilhelm S, Cameron-MacMillan ML, Walsh CJ, Storey AE, 2005. Divorce in common murrelets (*Uria aalge*): relationship to parental quality. *Behav Ecol Sociobiol* 57:224–230.
- Naves LC, Monnat JY, Cam E, 2006. Breeding performance, mate fidelity, and nest site fidelity in a long-lived seabird: behaving against the current? *Oikos* 115:263–276.
- Ramsay SM, Otter KA, Mennill DJ, Ratcliffe LM, Boag PT, 2000. Divorce and extrapair mating in female black-capped chickadees (*Parus atricapillus*): separate strategies with a common target. *Behav Ecol Sociobiol* 49:18–23.
- Ren QM, Luo S, Du XJ, Chen GL, Song S et al., 2016. Helper effects in the azure-winged magpie *Cyanopica cyana* in relation to highly-clumped nesting pattern and high frequency of conspecific nest-raiding. *J Avian Biol* 47:449–456.
- Richardson DS, Burke T, 1999. Extra-pair paternity in relation to male age in Bullock's orioles. *Mol Ecol* 8:2115–2126.
- Saether BE, 1990. Age-specific variation in reproductive performance of birds. *Curr Ornithol* 7:251–283.
- Smith RL, 1984. *Sperm Competition and the Evolution of Animal Mating Systems*. London: Academic Press.
- Sundberg J, Dixon A, 1996. Old, colourful male yellowhammers, *Emberiza citronella*, benefit from extra-pair copulations. *Anim Behav* 52:113–122.
- Suter SM, Bielańska J, Rothlin-Spillmann S, Strambini L, Meyer DR, 2009. The cost of infidelity to female reed buntings. *Behav Ecol* 20:601–608.
- Triefenbach R, Itzkowitz M, 1998. Mate switching as a function of mate quality in convict cichlids, *Cichlasoma nigrofasciatum*. *Anim Behav* 55:1263–1270.
- Valcu M, Kempenaers B, 2008. Causes and consequences of breeding dispersal and divorce in a blue tit, *Cyanistes caeruleus*, population. *Anim Behav* 75:1949–1963.
- Zabala J, Zuberogoitia I, 2015. Breeding performance and survival in the peregrine falcon *Falco peregrinus* support an age-related competence improvement hypothesis mediated via an age threshold. *J Avian Biol* 45:141–150.

