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High divorce rates in Corsican blue tits: how to choose a better option in a harsh environment

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We investigate which hypothesis, the "better mate hypothesis" or the "better territory hypothesis" best explains the unusually high divorce rate (59%) in a population of blue tits (*Parus caeruleus*) living in a sclerophyllous habitat characterised by severe environmental constraints (trophic, parasitic, climatic) on the island of Corsica, France. Using data from the breeding seasons 1985–1998 and from a brood size experiment (1990–1993) we examined the causes of divorce and their consequences on breeding performance, mate assortment and territory choice. Breeding performance had no significant effect on whether birds re-united or divorced in the next breeding season. Re-uniting pairs did better than divorced females and the latter improved their breeding performance compared to prior to divorce, but this was mainly due to age and territory effects. There were no differences in male performance depending on whether they re-united or divorced. The age combination of pairs did not differ between re-uniting and divorcing pairs, but mate assortment changed after divorce with males re-mating more often with older partners than females. Manipulation of brood size showed a trend for birds with enlarged broods to divorce more. Pairs responded significantly to territory quality by divorcing more often in poor than in good breeding sites. Both faithful pairs and male divorcees had shorter breeding dispersal distances than female divorcees. Divorce rates were determined by the large differences in quality among breeding sites. Males, whatever their status, usually retained their previous territory whereas divorced females moved significantly longer distances and improved their breeding site. Moving to a better territory after divorce benefits only females which appear to be the choosing sex in the decision to divorce. This study strongly supports the "habitat mediated hypothesis" and we suggest that the large observed intraspecific variation in the magnitude of divorce rates in many species of birds is mostly determined by habitat characteristics.

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A large number of studies have focused on partnership, mate choice and divorce in birds (see reviews by Rowley 1983, Black 1996, Ens et al. 1996). Divorce occurs when both partners of a pair survive to the next breeding season and so could potentially re-unite but choose to breed with another partner. The proximate causes of divorce may be purely passive, without any element of choice. This could typify nomadic or migratory species without site fidelity, short-lived species which take the first available partner to avoid the risk of mating late in the season while waiting for the unlikely return of a previous partner (Perrins and McCleery 1985, Linden 1991) or birds which, by chance, failed to find their previous partner (Owen et al. 1988; see also Dhondt and Adriaensen 1994). In these cases, divorce is non-adaptive. Divorce may be adaptive, however, when it results from the decision to break the pair-bond, as occurs when both partners have the opportunity to re-unite but do not. Several studies in recent years have shown that divorce rates vary greatly among species (from 0 to 100%) and among populations within species (see Ens et al. 1996). For example, divorce rates have

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been reported to vary from 8% to 85% and from 0% to 51% in several populations of blue tits (*Parus caeruleus*) and great tits (*Parus major*), respectively, in Belgium (Dhondt and Adriaensen 1994, Dhondt et al. 1996). Such a variation suggests that divorce is both species-specific and population-specific, and is related to environmental or demographic features. Mating for several breeding attempts with the same partner is usually advantageous for a number of reasons (see Rowley 1983, Black 1996, Ens et al. 1996). Familiarity between partners saves time involved in courtship and allows them to keep better breeding sites. Experienced adults that repeatedly re-unite often occupy better breeding sites, lay earlier in the season, and produce larger clutches (Perrins and Moss 1974, Bryant 1979). Therefore re-uniting should be favoured when both partners of a pair are still alive. On the other hand, divorce is expected to incur a cost. It may be difficult to find a new mate and the new pairing may involve longer courtship and pair formation processes, especially if the breeding site is unfamiliar and the new partner is young and inexperienced. These disadvantages explain why newly formed pairs often have lower breeding success than pairs which remain together for a long time (Coulson 1966, 1972, Mills 1973, Perrins and McCleery 1985). If divorce incurs a cost, then why do birds divorce frequently? Contrary to non-adaptive divorce where divorced and faithful pairs should not differ significantly in their reproductive performance between successive breeding attempts, adaptive divorce implies that advantages of re-mating with a new partner should be greater than costs, at least for one member of the original pair (see Coulson and Thomas 1983, Diamond 1987, Linden 1991). Divorce could be a response to poor breeding success the previous year and may be advantageous if an individual gains access to a better breeding site and/or mate (Grant and Grant 1987), and benefits from better reproductive success (Källander 1983).

No fewer than eleven different hypotheses have been proposed to explain adaptive divorce in birds (Choudhury 1995, Ens et al. 1996). Divorce was first thought to result from incompatibility between partners, in which case divorce would benefit both of them (Coulson 1966, 1972). More recently the "better option hypothesis" that emerged from behavioural observations on oystercatchers (*Haematopus ostralegus*) by Ens et al. (1993) suggests that one member of a pair makes the decision to divorce to improve its own reproductive success while leaving the previous partner as a victim. In this hypothesis, at least one member of the pair should improve its reproductive success by breeding with a better partner (the "better mate hypothesis") or in a better territory (the "better territory hypothesis"), a distinction which has not received much attention in the literature (Desrochers and Magrath 1996). The decision to divorce may result from several causes. Birds may avoid re-uniting with an adulterous mate or one providing poor parental care (Alatalo et al. 1984, Linden 1991, Birkhead and Møller 1992). Birds may try to improve their own fitness through a better genetic quality of their partner and offspring (Birkhead and Møller 1992). If breeding success is closely related to territory quality, a bird may try to occupy a better site, eventually divorcing if changing site implies changing mate (Greenwood and Harvey 1982). All these hypotheses rely on the existence of extensive variation in mate quality and severe intrasexual competition (Birkhead and Møller 1992, Choudhury 1995), especially if, as suggested by Ens et al. (1993), mates of high quality are in short supply in most populations of birds. The adaptive significance of divorce is supported by the fact that divorce occurs more often after unsuccessful breeding attempts (Rowley 1983, Diamond 1987, Linden 1991). If divorced birds enjoy a greater increase in success than birds that re-unite with the same partner, then there is an adaptive advantage of divorce.

To understand the ultimate significance of divorce we need to assess the trade-offs between costs and benefits associated with divorce. One obstacle to assess what drives a bird to desert its partner lies in the fact that although birds may show increased breeding success following divorce one cannot exclude the possibility that they would have had even better success had they remained faithful. There are two ways to circumvent this problem. The comparative method is based on changes in breeding performance from one breeding attempt to the next between divorced and faithful pairs (Källander 1983) while the experimental method requires manipulation of brood size and hence breeding performance to explore the causal force driving divorce (Linden 1991). If the decision to divorce is driven by breeding success, responses to manipulation should give an insight on the backgrounds of divorce.

In this paper we address the causes and effects of divorce using a long-term study of a population of blue tits living in a sclerophyllous evergreen oak forest on the island of Corsica. Compared to populations in deciduous oak habitats which are of much better quality for tits (Blondel et al. 1993, Lambrechts et al. 1997), this population lives in a harsh environment with severe environmental constraints which include not only a low food supply but one that becomes only available late in the season (one month later than in deciduous oakwoods), thermal and water constraints (Nager and Wiersma 1996), and high parasite loads (Hurtrez-Boussès et al. 1997; see Blondel et al. 1993, 1998, Lambrechts et al. 1997 for details). As a result of these constraints this population is characterised by the latest onset of breeding and the lowest clutch size so far recorded in Europe. In this habitat, population density of blue tits is fairly high and birds are more or less sedentary, spending the non-breeding season foraging over a wide home range shared with several other pairs.

In this paper, we address the following questions. Is divorce advantageous? Do individuals who divorce increase their reproductive success relative to that of the year preceding divorce? Are the benefits of either faithfulness or divorce equal between the two sexes? Does the probability of divorce change with age, with pairs including a young partner divorcing more frequently than older, more experienced birds? We also attempt to determine whether the primary cause of divorce is mate or territory quality, in an effort to compare the "better mate" and "better territory" hypotheses.

Material and methods

We used data for the breeding seasons 1985–1998 in a study area of ca 70 ha equipped with a superabundance of nestboxes (ca 2 nestboxes ha^{-1}). On average ca 60 pairs of blue tits breed annually in the study area and almost all of them occupy our nestboxes. Nestboxes were routinely checked and laying date (first egg), clutch size, hatching date, number of hatchlings and fledglings were recorded. Adults were caught when nestlings were close to fledging, identified from their ring number if ringed, sexed, and aged as yearlings (birds born the previous year) or older birds. Only first clutches were considered because renesting is rare in this population. We use the term "status" to refer to either divorced or faithful birds. Because many birds that bred in the study area for several years changed their status several times in the course of their breeding life (up to 10 yr), divorce rates were scored using the first observation per individual bird or pair whose status was known for more than two years. However, all the observations were used for analysing the effects of territory quality on the status of individual birds. Sample sizes for divorced birds differed between the sexes because of different individual histories and longevity. For example, a female who divorced and re-mated with a yearling male would score as divorced while her new mate would score as faithful if this new pair remained stable to the following year. Breeding dispersal was calculated as the distance between nestboxes used in two consecutive years. In this study area where nestboxes are ca 50 m apart, each territory includes up to three nestboxes so we assume that a breeding dispersal of less than 100 m means retention of the territory. However, pairs of blue tits can settle in two adjacent nestboxes in the same breeding season.

We used a brood size experiment conducted during the years 1990–1993 to investigate the effects of modifying breeding success on divorce rates. Manipulation involved two 2-d chicks randomly chosen and transplanted to create reduced or enlarged broods. This data set included 68 reduced and 68 enlarged broods (see Blondel et al. 1998 for details). Manipulated broods were used only for calculating divorce rates in relation to manipulation but they were not included in the analyses of breeding performance in relation to status and territory quality.

We normalised most variables (laying date, clutch size, fledging success) to take into account year effects by subtracting the yearly mean values from the measured values and dividing the difference by the standard deviation. In some analyses, we also controlled for variation in clutch size because there is a calendar effect of decreasing clutch size as laying date increases ($F_{1,623} = 81.4$, $P < 0.0001$). A problem in analyses of divorce is that age of the birds affects reproductive success. Therefore, we controlled for age of the birds in all analyses by including age (yearlings and older birds) as a covariate in the models.

Because there was no way to assess the quality of a territory, we used the quality of breeding sites (nestboxes) which has been defined as the fledging success of a given pair relative to the average success of all pairs in which both the female and the male were yearlings, and we weighted this value by the occupancy rate of the nestboxes over the whole study period (see Lambrechts and Dhondt 1988). We defined two breeding site classes. Poor quality sites had fledging success $< 50\%$ (99 sites) while high quality sites had fledging success $> 50\%$ (40 sites). The average value of fledging success was 37% in the former and 80% in the latter. Occupancy rates amounted to 72% of breeding opportunities (boxes × years) in good breeding sites against 37% in poor ones. However, since the study area was saturated with nestboxes, each blue tit territory includes several nestboxes between which pairs may shift so that nearly all good territories were occupied each year, sometimes with more than one pair per "territory" as defined above.

For most analyses, we used generalised linear models (GLIM, NAG 1986). We constructed maximal models including all the explanatory variables and used a stepwise backward deletion of variables with non-significant effects. Adjustment of the scale parameters was used to correct for overdispersion in some models (Aitkin et al. 1989). Statistical procedures were performed following Crawley (1993). Exact probabilities were calculated using StatXact. All tests are two-tailed. In this paper we use the term breeding performance to refer to the combined effects of laying date, clutch size and brood size (good breeding performance involves an early laying date and large clutch and brood size) and reproductive success to refer to the number of young fledged.

Results

In this population divorce rates were 59.1% ($N = 137$). Most birds with a known status for several years changed their mate several times in the course of their breeding life. The record was held by a male whose status was known for ten years. He divorced after his first breeding attempt, then remained with the same female for five consecutive years, and divorced again each year for the three next consecutive years. Some birds known for more than three years either consistently divorced or remained faithful at each breeding attempt. The mean pair duration for 248 pairs was 1.62 ± 0.72 yr and there was no significant difference between males and females in the number of partners during their residency on the study plot (males = 1.47 ± 0.79, females = 1.57 ± 0.84, Fisher exact test, $P = 0.14$). Divorce probabilities did not vary with the age of individuals or previous status (logistic regression, males $\chi^2 = 0.02$, $P = 0.88$, females $\chi^2 = 0.54$, $P = 0.46$). "Old faithful" pairs were not more likely to remain faithful than "young faithful" pairs or divorced birds, whatever their age.

Breeding performance of blue tits in relation to their mating status

Since our data were normalised, breeding performance in relation to mating status is compared to zero which is the average value of the total population, including birds of unknown status. Although complete breeding failure has been reported as a possible cause of divorce (Linden 1991, Dhondt and Adriaensen 1994), pairs that experienced complete failure ($N = 16$) were not more likely to divorce than those which fledged at least one offspring ($N = 121$) ($\chi^2 = 2.28$, $P = 0.96$).

Compared to pairs that re-united for the subsequent breeding event, pairs that divorced started on average to lay slightly later, had a slightly smaller clutch size, but fledged on average as many young and recruited a similar number of offspring (Table 1). Pairing status as a main effect did not influence breeding performance, except for number of fledglings (but see below), and most of the differences were due to age effects except for clutch size which did not significantly vary whatever the status and age of the birds. On average, adult females did better than yearling females, especially if

Table 1. Differences in breeding performance of blue tit pairs depending on whether they re-unite (F-1) or divorce (D-1) the year after. Data are given in relation to the population mean. A full model included mating status, female age, male age and their interactions. Factors with significant effects were reintroduced in the model. Results of main effects and their interactions (GLIM) are given below the mean values (normal error for laying date, clutch size and fledging success, binomial error for recruitment rate). Fage1 = adult female, Fage2 = yearling female, Mage1 = adult male, Mage2 = yearling male.

	Re-unite (F-1)			Divorce (D-1)		
	Mean	SE	P (t-test)	Mean	SE	P (t-test)
Laying date						
Overall	−0.031	0.133	NS	0.199	0.112	NS
Fage1 – Mage1	−0.345	0.234	NS	−0.006	0.234	NS
Fage1 – Mage2	−0.314	0.444	NS	0.608	0.444	NS
Fage2 – Mage1	0.109	0.234	NS	0.264	0.173	NS
Fage2 – Mage2	0.271	0.256	NS	0.270	0.217	NS
Status, $F_{2,572} = 0.769$, $P = 0.468$; female age, $F_{2,574} = 5.232$, $P = 0.006$; male age, $F_{2,574} = 0.523$, $P = 0.599$; female age × status, $F_{7,571} = 2.103$, $P = 0.041$.						
Clutch size						
Overall	0.114	0.134	NS	−0.026	0.112	NS
Status, $F_{2,577} = 0.587$, $P = 0.562$; female age, $F_{2,575} = 1.956$, $P = 0.562$; male age, $F_{2,573} = 1.779$, $P = 0.167$.						
Number of fledglings						
Overall	0.363	0.130	0.007	0.393	0.109	<0.001
Fage1 – Mage1	0.748	0.197	0.001	0.361	0.197	0.083
Fage1 – Mage2	0.586	0.374	NS	0.512	0.374	NS
Fage2 – Mage1	0.341	0.197	NS	0.441	0.146	0.005
Fage2 – Mage2	−0.147	0.216	NS	0.237	0.183	NS
Status, $F_{2,572} = 3.836$, $P = 0.022$; female age, $F_{2,574} = 23.02$, $P < 0.0001$; male age, $F_{2,574} = 15.78$, $P < 0.0001$; female age × status, $F_{7,571} = 30.89$, $P < 0.0001$; male age × status, $F_{7,571} = 27.81$, $P < 0.0001$; female age × male age × status, $F_{18,560} = 14.73$, $P < 0.0001$.						
Number of recruits	0.049	0.015	0.002	0.044	0.013	0.001
Status, $\chi^2_2 = 3.95$, $P = 0.139$; female age × status, $\chi^2_7 = 59.84$, $P < 0.0001$; male age × status, $\chi^2_7 = 47.72$, $P < 0.0001$; female age × male age × status, $\chi^2_{18} = 74.79$, $P < 0.0001$.						

Table 2. Age composition of blue tit pairs according to their status. Figures in parentheses correspond to the total numbers of birds which were either yearlings or older prior to divorce. Same symbols as in Table 1.

Age composition	F-1	D-1	D-Females		D-Males	
Fage1 – Mage1	18	19	56	(52)	54	(26)
Fage1 – Mage2	5	7	25	(29)	–	–
Fage2 – Mage1	18	33	–	–	27	(55)
Fage2 – Mage2	15	22	–	–	–	–
Total	56	81	81	81	81	81

Differences in age composition between F-1 and D-1 pairs, $\chi^2 = 1.587$, $P = 0.662$; between D-1 and D females, $\chi^2 = 0.250$, $P = 0.617$; between D-1 and D males, $\chi^2 = 18.00$, $P < 0.0001$.

their mate was also an adult. Pairs composed of yearlings tended to do worse than the population average whatever their mating status. However, there was a significant interaction between the age of the female and status for laying date, and between the age of both partners and status for the number of fledglings and recruits. Old females that re-united laid significantly earlier than old females that divorced, but yearling females that divorced fledged and recruited more offspring in the year prior to divorce than those that subsequently re-united (results shown only for fledging success in Table 1). Interestingly, both categories with known pairing status, either faithful or divorced, fledged significantly more offspring than birds of unknown status (-0.117 ± 0.046, $P = 0.011$). This difference explains the significant effect of status either as a main factor (number of fledglings) or in interaction with age in the analyses. Reanalysing the effects of status without incorporating birds of unknown status showed that both faithful and divorced pairs had a similar fledging success ($F_{1,134} = 0.043$, NS) and recruitment rate ($\chi^2 = 0.739$, NS). Our results do not show any clear differences in reproductive performance in relation to whether pairs will remain together or separate.

Age composition of pairs in relation to status

Since the interaction age × status affected breeding performance (except for clutch size), we examined whether the age composition of partners within a pair affected divorce rate, e.g., whether divorced birds tried to improve their mating status by selecting more experienced, older partners. The age composition of pairs did not differ significantly in relation to whether they re-united or divorced in the next breeding season (F-1 vs D-1 in Table 2). Females that divorced were not mated significantly more often with yearling males than those that re-united ($\chi^2 = 0.07$, $P = 0.79$). However, mate assortment strongly changed in the next breeding season for divorced birds. Divorced females, either adults or yearlings prior to divorce, did not re-mate significantly more often with adult males (56 divorced females vs $19 + 33 = 52$ females prior to divorce, see Table 2) than with yearling males (25 divorced females vs $7 + 22 = 29$ females prior to divorce) whereas divorced males re-mated significantly more often with adult females (54 divorced males vs $19 + 7 = 26$ males prior to divorce) than with yearling females (27 divorced males vs $33 + 22 = 55$ males prior to divorce). As a result, excluding pairs where both partners were yearlings (which by definition does not exist among divorced birds) there were more pairs with the two sexes as adults in divorced pairs (69.1% for divorced females and 66.7% for divorced males) than in pairs prior to divorce (32.2%) ($\chi^2_4 = 35.1$, $P < 0.0001$). The difference is mostly due to males re-mating more often with adult females.

Breeding parameters of divorcees and faithful pairs

We next examined the consequences of re-uniting or divorcing on breeding performance by calculating changes in breeding performance (normalised values) between two successive breeding attempts. Again, status as a main factor had no significant effect on breeding performance for either females or males (Table 3). Divorced females tended to improve their performance for laying date and clutch size, but not for fledging success. The only significant factor was age of the female as a main factor and in interaction with status (except for clutch size). Faithful females tended to do better than divorced females, but reproductive success did not improve with increasing number of years with the same partner. Changes in performance of males in relation to status were similar to those of females with age of the female being the only significant factor (except for clutch size).

Mating status in relation to brood size experiment

For the 136 broods that were manipulated between 1990 and 1993, mating status the year after the experiment was known for 37 pairs. In all years, reduced broods fledged fewer and enlarged broods more offspring than controls (see Blondel et al. 1998). Divorce rates were 47%, 22% and 73% for reduced, controls and enlarged broods, respectively, but the trend of more

Table 3. Changes in breeding performance (SE = Standard error) of female and male blue tits between two successive breeding seasons according to their status of faithful (F) or divorcees (D). Same models as in Table 1. $^{*}P<0.05$, $^{**}P<0.001$.

	F-1	F	D-1	D
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Females				
Laying date				
Fage1	−0.358 (0.194)	−0.286 (0.127)*	0.116 (0.190)	−0.131 (0.106)
Fage2	0.356 (0.171)*		0.371 (0.132)**	
Status, $F_{3,273} = 0.855$, $P = 0.455$; female age, $F_{1,273} = 6.270$, $P = 0.013$; male age, $F_{1,272} = 1.468$, $P = 0.231$; female age × status, $F_{5,272} = 4.772$, $P = 0.0004$.				
Clutch size	0.079 (0.133)	0.015 (0.132)	−0.092 (0.112)	0.024 (0.110)
Status, $F_{3,274} = 0.363$, $P = 0.783$; female age, $F_{1,273} = 0.015$, $P = 0.902$; male age, $F_{1,272} = 0.642$, $P = 0.424$.				
Fledglings				
Fage1	0.411 (0.198)*	0.149 (0.130)	0.084 (0.194)	−0.103 (0.109)
Fage2	−0.345 (0.175)*		−0.027 (0.135)	
Status, $F_{3,273} = 1.536$, $P = 0.204$; female age, $F_{1,273} = 5.049$, $P = 0.025$; male age, $F_{1,272} = 2.512$, $P = 0.114$; female age × status, $F_{5,272} = 2.187$, $P = 0.055$.				
Males				
Laying date				
Fage1	−0.443 (0.170)**	−0.256 (0.127)*	0.080 (0.145)	−0.160 (0.136)
Fage2	0.449 (0.189)*		0.462 (0.170)**	0.267 (0.189)
Status, $F_{3,263} = 1.379$, $P = 0.248$; female age, $F_{1,263} = 15.25$, $P = 0.0001$; male age, $F_{1,262} = 0.810$, $P = 0.369$.				
Clutch size	0.167 (0.131)	0.075 (0.132)	−0.149 (0.114)	−0.033 (0.114)
Status, $F_{3,264} = 1.242$, $P = 0.294$; female age, $F_{1,263} = 1.268$, $P = 0.261$; male age, $F_{1,262} = 1.379$, $P = 0.241$.				
Fledglings				
Fage1	0.247 (0.174)	0.180 (0.130)	−0.068 (0.148)	0.192 (0.139)
Fage2	−0.367 (0.193)		−0.386 (0.174)*	−0.103 (0.189)
Status, $F_{3,263} = 1.011$, $P = 0.389$; female age, $F_{1,265} = 8.131$, $P = 0.004$; male age, $F_{1,265} = 0.562$, $P = 0.454$.				

birds being faithful in reduced broods and more birds divorcing in enlarged broods is not significant (Table 4).

Breeding performance in relation to mating status and territory quality

Although the study area seems at first view relatively homogeneous, breeding sites differ greatly in quality (see Material and methods). Good breeding sites have higher nestbox occupancy rates, earlier laying date, larger clutch size, better quality fledglings (estimated by body mass and tarsus length at the age of 15 d) and tend to recruit more offspring than do poor territories (Table 5). These differences were consistent over years and did not arise because the same individuals remained in the same territory year after year. In order to test the "better territory hypothesis", we examined whether the best territories were occupied by faithful pairs who retained them longer, and whether divorced birds shifted from poor to good territories. Pairs did respond to territory quality by divorcing more often in poor than in high quality breeding sites ($\chi^2 = 6.31$, $P = 0.012$, Fig. 1). Faithful pairs that changed their nestbox between two consecutive breeding events did not improve their territory quality significantly ($\chi^2 = 0.201$, $P = 0.653$, Fig. 1), primarily because they remained in their previous territory. On the other hand, divorced females significantly improved their breeding site by moving to a better one ($\chi^2 = 6.43$, $P = 0.011$, see Fig. 1) but divorced males did not ($\chi^2 = 0.02$, $P = 0.965$). Thus, changing partner appears to reflect a female's decision to move to a better territory. Site fidelity is high in blue tits, especially when breeding has been successful. Both faithful pairs and male divorcees had shorter breeding dispersal than female divorcees (Kruskall-Wallis, $H = 49.5$, $P < 0.001$). The median breeding dispersal distance of faithful pairs was 37.0 m (range 0–210 m), which means that most of them remained within the limits of their territory although they often changed their nestbox from one breeding attempt to the next. Divorced birds changed breeding sites more often than faithful pairs (74% of divorced birds changed against 54% of faithful pairs, Fisher exact test, $P < 0.001$). Divorced males moved slightly

Table 4. Mating status in the year following brood size manipulation (two chicks removed from or added to nests). For pairs that bred more than two consecutive years in the study area, only status the year after the first experiment has been considered.

	Experimental groups		
	−2	0	+2
Divorce	8	2	7
Mate fidelity	10	7	3

$\chi^2 = 4.38$, $P = 0.112$.

Table 5. Breeding performance of blue tits in relation to breeding site quality (normalised values ± SE). Binomial error for numbers of hatchlings and recruits, normal error for other parameters. The models controlled for age of the female.

	Poor quality	Good quality	Statistics
	Mean ± SE	Mean ± SE	
Laying date	0.095 ± 0.048	−0.121 ± 0.055	$F_{1,752} = 6.632$, $P = 0.01$
Clutch size	−0.069 ± 0.048	0.090 ± 0.055	$F_{1,752} = 4.737$, $P = 0.03$
Hatchlings	0.832 ± 0.012	0.859 ± 0.450	$\chi^2 = 2.9$, $P = 0.088$
Recruits	0.031 ± 0.004	0.041 ± 0.050	$\chi^2 = 3.34$, $P < 0.068$
Fledgling mass	−0.145 ± 0.066	0.157 ± 0.068	$F_{1,431} = 10.12$, $P = 0.001$
Fledgling tarsus	−0.168 ± 0.075	0.199 ± 0.081	$F_{1,311} = 10.95$, $P = 0.001$

but significantly longer distances than males of faithful pairs (median, 45 m, range 0–300 m, Wilcoxon-Mann-Whitney, $Z = 2.425$, $P < 0.05$) but most of them still remained within the limits of their territory. On average, divorced females moved much longer distances than divorced males and faithful females (median 90 m, range 0–877 m, $Z = 6.722$, $P < 0.001$) and most of them changed their territory. It is interesting to note that pairing status does not affect the reproductive success of birds occupying good territories (Fig. 2), but the key point is that explanatory variables of changes in breeding performance for various breeding parameters in relation to status were not the same for faithful pairs and divorced birds. Changes in performance were due to age effects for faithful pairs and divorced males whereas they were mostly due to status and breeding site quality for divorced females (see caption of Fig. 2). Thus moving from one territory to another after divorce benefits only the female.

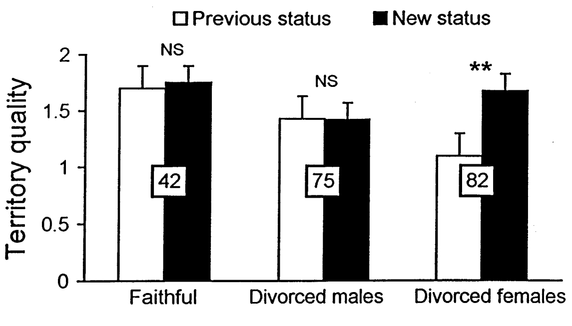

Fig. 1. Breeding site quality of faithful pairs, divorced males and divorced females between two consecutive breeding attempts. Samples sizes in the columns. **, $P < 0.001$.

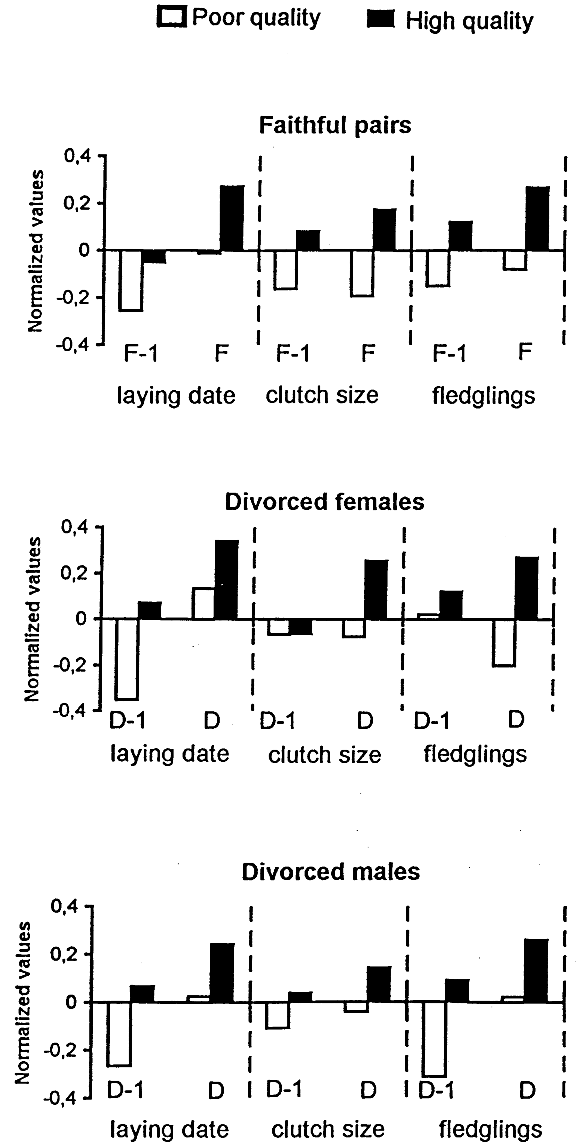

Fig. 2. Changes in breeding performance of blue tits between two consecutive breeding attempts according to status (F-1 = re-uniting, D-1 = divorcing birds) and breeding site quality. In order to show all changes as positive values we used the inversed laying date (laying date^{-1}). For faithful pairs and divorced males significant effect was age of the female (laying date, $F = 6.491$, $P = 0.012$, $F = 5.28$, $P = 0.023$ respectively; fledglings, $F = 7.288$, $P = 0.008$, $F = 3.847$, $P = 0.051$ respectively). For divorced females significant effect was the interaction status × site quality (laying date, $F = 4.334$, $P = 0.006$; fledglings, $F = 3.151$, $P = 0.026$).

Discussion

The divorce rate of 59% in this Corsican population of blue tits is much higher than those reported in several other European populations of tits, e.g., the great tit, the coal tit (*Parus ater*), or the blue tit where divorce rates were, with few exceptions (see Introduction), of the order of 20–40% (Dhondt and Adriaensen 1994, Dhondt et al. 1996; see also Cézilly and Nager 1995). Such high divorce rates were unexpected in this population because pairs that remained together had better breeding performance than divorcees and both sedentariness and site fidelity which characterise Corsican tits should favour the maintenance of the pair-bond because contrary to migratory birds, there is no risk of divorce arising from differences in the timing of returning from winter grounds. Dhondt et al. (1996) suggested that the more resident the population, the lower the divorce rates because divorce rates strongly depend on winter social behaviour with winter flocking and dispersal in poor quality habitats favouring the search of better partner, hence increasing divorce rates. In Corsica where birds may remain together all year round and usually do not flock in the non-breeding season, finding a new partner should be costly because females must visit a series of males one after the other and so run the risk of being deserted by their previous partner (Ens et al. 1993).

This study produced several striking results. First, the differences in breeding success in relation to whether birds will re-unite or divorce are mostly explained by age combinations within pairs, old birds doing much better than young ones. Thus, breeding success in the current breeding season does not explain future pairing status. Second, status as a main factor does not explain changes in breeding success between two consecutive breeding attempts. Third, there was no relationship between divorce probabilities and the age composition of pairs in the previous year nor was there any significant trend of a decrease in divorce rates with age of females (divorce rates were 51% for adults and 62% in yearlings, Fisher exact test, $P = 0.116$). Fourth, although there was a clear advantage for pairs to remain faithful since, on average, they produce more offspring than those that divorce, many pairs that remained faithful for several years (10 for 2 yr, 5 for 3 yr, 2 for 4 yr and 1 for 5 yr) did not improve their breeding success through time and many of them still divorced after several years of faithfulness. Fifth, brood size experiments hardly revealed any significant effects of previous breeding success on the decision to divorce. Sixth, both faithful pairs and male divorcees retained their territory while female divorcees changed and, on average, significantly improved their breeding territory, hence their breeding success. Our results differ from those of Dhondt and Adriaensen (1994) for Belgian blue tits and of Linden (1991) for Scandinavian great tits. Dhondt and Adriaensen showed that compared to pairs that remained together, birds that divorced had lower breeding performance but reproductive success improved after divorce for females (but not for males). In a Scandinavian population of great tits Linden (1991) also found that pairs producing more offspring than the average (enlarged broods as compared to controls) divorce less, a pattern which is not confirmed in our study of Corsican tits.

An explanation for the high divorce rate in our Corsican population may lie in the large variation in breeding site quality and/or partners. Although our categorisation of nest site quality is admittedly rather crude (only two classes), poor breeding sites by far outnumber good ones (99 vs 40). Several arguments suggest that severe competition for high quality nest sites drives the observed high divorce rate and that females rather than males make the decision to divorce and move to better breeding situations. First, territory quality has a clear effect on breeding performance as well as on mate assortment. Second, faithful pairs tend to occupy the best territories and remain within them over years so that what appears to be advantages of mate fidelity could in fact be the advantages of site fidelity (pairing status as a main factor had no effect). Interestingly, the fact that pairs that re-united did not move more often to better breeding sites (see Fig. 1) suggests that only those pairs that had a good chance to improve their breeding site did move, which is an indication of competition for good nesting sites. Third, males, whatever their status, usually retained their previous territory. The 40 best sites of our study area were consistently occupied by adult males whereas the poorest sites were occupied by young males ($\chi^2 = 7.43$, $P = 0.006$). Fourth, divorced females moved significantly larger distances than divorced males and improved on average their breeding site and therefore their breeding situation. Thus divorce is more likely in pairs that were established in poor territories. It is not clear why there was no direct effect of status on breeding performance for divorced females (Table 2) since on average they improved their breeding success. The most likely explanation is that for unknown reasons, divorced females settling in poor quality sites did even worse than prior to their divorce (see Fig. 2).

Although the age composition of pairs did not significantly affect the probability of divorce, this does not necessarily mean that the age composition of pairs was not a cause of divorce. For divorced females, the cost of mating with a yearling male should be small since there were no effects of male age on reproductive success but for divorced males, mating with a young inexperienced female should be much more costly (Desrochers and Magrath 1996). Indeed, divorced males but not divorced females took significantly more often old partners (67.5% of 80 divorced males re-mated with old females as compared to 51.8% of 108 divorced females re-mating with older males). This suggests that females compete for older males and make the decision to divorce rather than the other way around. The most likely explanation for divorced females not re-mating more often with old males is that the combination of an old male and a high quality territory is limited so not all females can express their preference. Since in the blue tit males are dominant over females and show strong site fidelity, a decision to divorce means that the female has to leave her territory in order to obtain a new mate. As a result females are often forced to pair with suboptimal males (or males holding poor quality breeding sites) and take the first opportunity to improve their breeding situation (Johnston and Ryder 1987, Sullivan 1994), eventually by displacing a male's previous mate ("forced divorce hypothesis"). The reasons why females rather than males take the decision to divorce are that (1) females suffer a lower cost of divorce because the age of males has little effect on reproductive success, and (2) territorial defence is the role of the male so that the cost of moving should be smaller for females (Desrochers and Magrath 1996). We cannot exclude, however, that a male rejects his previous female and attracts a new one although such rejection of former mates has never been proved (Ens et al. 1996). Our conclusion agrees with those of many previous studies supporting the view that the female is the choosy sex (Källander 1983, Grant and Grant 1987, Linden 1991, Smith 1991, Dhondt and Adriaensen 1994, Orell et al. 1994).

It is difficult to make a distinction between the better mate hypothesis and the better territory hypothesis because high quality males are likely to be those that hold good territories (see Greenwood and Harvey 1982, Johnston and Ryder 1987). How birds can assess territory quality or mate quality is largely conjectural. One way that tits may evaluate territory quality is by examining the offspring production of pairs since the family group remains in the territory for several weeks after fledging (Desrochers and Magrath 1996). One other cue allowing females to assess male quality may be his ability to retain and defend his previous territory. If good, experienced males are more likely to occupy good sites, then the mechanism of active choice by females should be through mate quality. Females may also experience males of the neighbourhood through extra-pair fertilisation from better quality males than their own mate, which allows females to improve their breeding success in the current breeding season and helps them in finding a better partner for a subsequent breeding attempt as suggested by Cézilly and Nager (1995) who found a significant relationship between extra-pair paternity and divorce. Thus, if extra-pair paternity and divorce are associated in a two step process, the so called "sampling hypothesis" (Heg et al. 1993), high rates of extra-pair paternity are expected in this population. This may be especially true in this dense insular population where pairs of blue tits can occupy nest-boxes that are only 50 m apart, a situation never found on the mainland, and there is much overlap between territories. In such a situation females can observe and experience several males in their neighbourhood and take the first opportunity to mate with a better partner (see Kempenaers et al. 1992).

Dhondt and Adriaensen (1994) emphasised the large range of variation in divorce rates between and within species, which raises the question which hypothesis, the "better territory" of the "better mate" hypothesis, better explains divorce and whether the same explanation applies to all populations. There is actually much variation among populations in the probable causes of divorce. For example, low reproductive success prior to divorce has been reported in several studies (e.g., Linden 1991, Dhondt and Adriaensen 1994, Desrochers and Magrath 1996) but not in others (e.g., Harvey et al. 1979, Källander 1983, Perrins and McCleery 1985, Dhondt et al. 1996). Also brood size manipulation resulting in experimental changes in breeding success yielded divergent results in Linden's (1991) study in great tit and ours. It is interesting that females having experimentally enlarged broods had a higher divorce rate than females with reduced clutches. If good territories offer resources that better allow females to provision large broods, then females may seek to better match their reproductive effort (clutch size) and food supply by changing territory in subsequent years.

There is some evidence that habitat characteristics directly affect the occurrence of divorce and that divorce is more common in low quality and/or unstable habitats than in high quality and/or more predictable ones (Dhondt and Adriaensen 1994, Cézilly and Nager 1995). Recent studies on sparrowhawks (*Accipiter nisus*) (Newton and Wyllie 1996) and blackbirds (*Turdus merula*) (Desrochers and Magrath 1996) suggest that birds in poor quality habitats divorce more than those in high quality habitats. This "habitat-mediated hypothesis" (Newton and Wyllie 1996) suggests that divorce could be a side effect of females seeking to improve their breeding situation by moving from low quality to higher quality territories. Little attention has been paid to site choice but Alatalo et al. (1986) experimentally showed that female collared flycatchers (*Ficedula albicollis*) choose nest site characteristics rather than male phenotypes. In the same line, our study strongly supports the "habitat mediated hypothesis" which relies on there being consistent territory effects on reproduction. The role of mate quality remains unclear although it is likely that good territories are also those that are held by high quality males. We argue that the large observed intraspecific variation in the magnitude of divorce rates among bird species results from different proximate causes that are mostly determined by habitat characteristics. In this Corsican habitat characterised by severe environmental constraints where food supply is almost always a limiting factor (Blondel et al. 1991, Banbura et al. 1994; see also Nager and Wiersma 1996), improving breeding success is a challenge which birds must regularly confront. The high variation in territory quality with a relatively low number of good territories presumably exacerbates competition for sites and/or for partners, which explains why females so frequently divorce in their attempt to improve their own fitness, which fits the habitat component of the better option hypothesis.

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