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Mate fidelity and coloniality in waterbirds: a comparative analysis

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Abstract Increased opportunities for information are one potential benefit of sociality. We apply this idea to the advantages of colonial breeding in bird species that are typically monogamous within a breeding season but often form new pair-bonds in subsequent seasons. Individuals may benefit from nesting in colonies at high density by identifying good-quality potential alternative mates among their neighbours. The opportunities for finding a better mating option are likely to increase with colony size and density. We tested this prediction with a comparative analysis of the association between mate fidelity and coloniality in waterbirds (wading birds and seabirds), where there is wide variation in both the degree of mate retention over consecutive breeding seasons and the degree of coloniality. We used two comparative statistical analyses, one based upon generalized least squares and the other based upon a continuous-time Markov model, to test whether the pattern of association between divorce rate and degree of coloniality was evidence for correlated evolutionary change in the two characters. We found a significant and positive association between divorce rate and the degree of coloniality in waterbirds. The probable ancestral state corresponds to a combination of a high degree of coloniality with no, or weak, mate fidelity. The reconstruction of the historical pattern of character origin and evolution indicates that the transition from a high to a low degree of coloniality occurred before the transition to higher mate fidelity.

Key words Better option hypothesis · Coloniality · Comparative method · Monogamy · Waterbirds

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Introduction

Most long-lived "monogamous" bird species have more than one mate as an adult. As a consequence, much of mate choice concerns attempts at finding a new mate, or forming a pair-bond for a subsequent reproductive attempt (Rowley 1983; Choudhury 1995; Ens et al. 1996). Bird species vary widely in the degree of mate retention. In some species individuals tend to maintain a long-lasting pair bond (Tickell 1968; Richdale and Warham 1973), whereas in others, individuals experience several different partners during their reproductive lifespan (Aebischer et al. 1995; Cézilly and Johnson 1995).

Various factors, including longevity, habitat stability and biased sex-ratios have been proposed to explain the observed inter-specific variation in mate-retention over consecutive breeding attempts (Rowley 1983; Choudhury 1995). Mate switching or "divorce" between breeding seasons may be an adaptive strategy by which individuals increase their future breeding success (Diamond 1987). According to the "better option hypothesis" (Ens et al. 1993), divorce would be beneficial only to the individual who initiates the breaking of the pair-bond. Mate sampling may mean that some individuals end up paired with a "sub optimal" partner. Such individuals may then initiate the events that lead to divorce if they perceive an opportunity to pair with a new mate of better quality. Ens et al. (1993) suggested that such opportunities would be more frequent when adult mortality is high. They therefore predicted that across species the divorce rate would increase as adult survival decreased. A recent comparative analysis provided no evidence for an increase in divorce rate with mortality rate as originally expected (Ens et al. 1996).

For the "better option" hypothesis to work, individuals must have an opportunity to gain information about the quality of potential mates relative to the quality of their current partner. Increased opportunities for information are one potential benefit of sociality. For example, colonial birds may derive information about the location of food patches (Wittenberger and

Table 1 Divorce rate and degree of coloniality in monogamous colonial waterbirds. Studies with fewer than 10 pair-years were excluded. The degree of coloniality is 1 if species typically breed in large dense colonies. The degree of coloniality is 0 if species are facultatively colonial or form loose aggregations

Species	Latin name	Divorce rate	Degree of coloniality	Sources
Common murre	*Uria aalge*	0.19	1	Harris in Ens et al. (1996); Hudson (1985)
Black guillemot	*Cepphus grylle*	0.06	0	Peterson (1981); Asbirk (1979)
Cassin's auklet	*Ptychoramphus aleuticus*	0.07	1	Sydeman et al. (1996)
Crested auklet	*Aethia cristatella*	0.24	1	Jones (1993)
Least auklet	*Aethia pusila*	0.36	1	Jones & Montgomerie (1991)
Atlantic puffin	*Fratercula artica*	0.08	1	Ashcroft (1976)
Black-faced sheathbill	*Chionis minor*	1.00	1	Verheyden (1988)
South polar skua	*Catharacta maccormicki*	0.06	0	Pietz & Parmelee (1994); Wood (1971)
Great skua	*Catharacta skua*	0.45	0	Kepler (1969)
Arctic skua	*Stercorarius parasiticus*	0.17	0	O'Donald (1983)
Ring-billed gull	*Larus delawarensis*	0.28	1	Southern Southern (1982)
Glaucous-winged gull	*Larus glaucescens*	0.30	0	Vermeer (1963)
Silver gull	*Larus novaehollandiae*	0.07	1	Mills et al. (1996); Ottaway et al. (1988)
Black-legged kittiwake	*Rissa tridactyla*	0.23	1	Hatch et al. (1993); Coulson & Thomas (1983)
Caspian tern	*Hydropogne caspia*	0.50	1	Cuthbert (1985)
King penguin	*Aptenodytes patagonicus*	0.75	1	O. Olsson (pers. com.); Weimerskirch et al. (1992)
Emperor penguin	*Aptenodytes forsteri*	0.85	1	Isenman (1971)
Adelie penguin	*Pygoscelis adeliae*	0.34	1	Jouventin & Mougin (1981); Davis & Speirs (1990); Trivelpiece & Trivelpiece (1990); Ainley et al. (1983)
Gentoo penguin	*Pygoscelis papua*	0.27	0	Bost & Jouventin (1990); Williams & Rodwell (1992); Trivelpiece & Trivelpiece (1990)
Chinstrap penguin	*Pygoscelis antartica*	0.18	1	Trivelpiece & Trivelpiece (1990)
Rockhopper penguin	*Eudyptes chysocome*	0.21	1	Moors & Cunningham in Marchant and Higgins (1990)
Macaroni penguin	*Eudyptes chrysolophus*	0.09	1	Williams & Rodwell (1992)
Fiordland crested penguin	*Eudyptes pachyrhynchus*	0.09	0	Cassady St Clair et al. (in press)
Yellow-eyed penguin	*Megadyptes antipodes*	0.18	0	Darby & Seddon (1990)
African penguin	*Spheniscus demerus*	0.14	1	La Cock et al. (1987)
Magellanic penguin	*Spheniscus magellanicus*	0.10	1	Boersma & Fowler in Ens et al. (1996)
Galapagos penguin	*Spheniscus mediculus*	0.11	0	Reilly & Cullen (1981)
Little penguin	*Eudyptula mior*	0.03	0	Boersma (1976)
Wilson's storm petrel	*Oceanites oceanicus*	0.20	1	Beck & Brown (1970)
Leach's storm petrel	*Ocaenodroma leucorhoa*	0.05	0	Douglas et al. (1977)
Cape petrel	*Daption capense*	0.03	0	Sagar in Ens et al. (1996)
Southern giant petrel	*Macronectes giganteus*	0.16	0	Voisin (1988)
Northen giant petrel	*Macronectes halli*	0.14	0	Voisin (1988)
Northen fulmar	*Fulmarus glacialis*	0.04	0	Ollason & Dunnet (1978); Mc Donald (1977)
Southern fulmar	*Fulmarus glacialoides*	0.03	1	Weimerskirch (1990)
Sooty shearwater	*Puffinus griseus*	0.16	1	Richdale (1957)
Short-tailed shearwater	*Puffinus tenuirostris*	0.17	1	Bradley et al. (1990)
Manx shearwater	*Puffinus puffinus*	0.10	0	Brooke (1978)
Cory's shearwater	*Calonectris diomedea*	0.06	1	Mougin et al. (1987)
White-chinned petrel	*Procellaria aequinotialis*	0.07	1	Mougin (1970)
Wandering albatross	*Diomedea exultans*	0.00	0	Tickel (1968)
Laysan albatross	*Diomedea immutabilis*	0.02	1	Fisher (1975)
Waved albatross	*Diomedea irrorata*	0.00	0	Harris (1973)
Black-browed albatross	*Diomedea melanophris*	0.06	1	Prince et al. (1994)
Buller's albatross	*Diomedea bulleri*	0.00	0	Richdale & Warham (1973)
Yellow-nosed albatross	*Diomedea chlorohynchos*	0.04	0	Jouventin et al. (1983)
Sooty albatross	*Phoebetria fusca*	0.05	0	Prince et al. (1994); Jouventin & Weimerskirch (1984)
Greater flamingo	*Phoenicopterus ruber roseus*	0.99	1	Cézilly & Johnson (1995)
Grey heron	*Ardea cinera*	1.00	1	A. Block (pers. com)

Table 1 (continued)

Species	Latin name	Divorce rate	Degree of coloniality	Sources
Great blue heron	*Ardea herodias*	1.00	1	Simpson et al. (1987)
Northen gannet	*Sula bassana*	0.16	1	Nelson (1978)
Masked booby	*Sula dactylatra*	0.45	1	Kepler (1969)
Brandt's cormorant	*Phalacrocorax penicilatus*	0.63	1	Boekelheide & Ainley (1989)
European shag	*Phalacrocorax aristotelis*	0.36	1	Aebischer et al. (1995)
Antrcic shag	*Phalacrocorax bransfieldensis*	0.58	1	Bernstein & Maxson (1982)
Crozet shag	*Phalacrocorax melanogenis*	1.00	1	Derenne et al. (1976)
Flightless cormorant	*Phalacrocorax harrisi*	0.88	1	Harris (1979)
White-tailed tropicbird	*Phaeton lepturus*	0.08	0	Phillips (1987)

Hunt 1985) or about the quality of breeding sites (Forbes and Kaiser 1994; Boulinier and Danchin 1997) from conspecifics through local enhancement. We suggest that the same principles may apply to the evaluation of alternative breeding options. The evolution and maintenance of coloniality in birds has previously been interpreted in relation to mating advantages, in terms of mate choice (Draulans 1987), or in relation to the pursuit of extra-pair copulations by females (Wagner 1992; Hoi and Hoi-Letner 1997). However, colonial breeding and high nesting density may also help individuals to assess the relative performance of their reproductive partner simply by monitoring the performance of close neighbours. In addition, within colonies, individuals may identify good-quality individuals among their neighbours and thus evaluate alternative pairing options.

The opportunities for finding a better option are likely to increase with colony size and density because close proximity with conspecifics makes it easier to assess neighbours' quality, and increases the number of possible alternative pairing options. To test this idea, we perform a comparative analysis of the association between mate fidelity and coloniality in colonial waterbirds, that is the wading birds and seabirds. Most species in this group are monogamous, with parental care shared between the two parents (Del Hoyo et al. 1992, 1996). The degree of mate retention over consecutive breeding seasons (Warham 1990; Cézilly and Johnson 1995; Williams 1995) varies widely. The degree of coloniality also varies among colonial waterbirds, with some species forming large and dense colonies while others typically form loose agregations of a few nests (Siegel-Causey and Kharitonov 1990).

Here we use phylogenetically based comparative statistical analyses of waterbirds to test for a relationship between mate fidelity and the degree of coloniality. Our analyses allow us to test not only for an association between these two traits but also to identify the temporal sequence of changes as they evolved from their ancestral conditions.

Methods

Data on divorce rate and degree of coloniality were collected from the literature and from other investigators for 58 species, belonging to 14 families and 6 orders (Table 1). Data on divorce were included in the analysis only if they corresponded to the case when at least one partner re-paired and bred with a different partner the following year, while the previous mate was still alive and present in the population. We did not consider divorce within the breeding season in this analysis. Divorce rates were calculated on a per year basis and were expressed as a continuous variable ranging from 0 (absolute mate fidelity) to 100 (no mate fidelity). In order to approximate to the normal distribution, data on divorce rates were transformed as log (divorce rate + 1). This transformation provided a better fit to the normal distribution than other transformations including Arcsin.

Coloniality was measured as a categorical variable because variation exists within some species in colony size and density. Based on the available literature (Del Hoyo et al. 1992, 1996; Warham 1990), we considered two categories. The first category (coloniality coded as 0) corresponds to species that are loosely colonial, i.e. that form aggregations of a few nests and/or have a low nesting density. The second category (coloniality coded as 1) corresponds to species typically nesting in large, dense colonies with internest distance usually not exceeding nest diameters by 1–2 orders of magnitude (see Siegel-Causey and Kharitonov 1990).

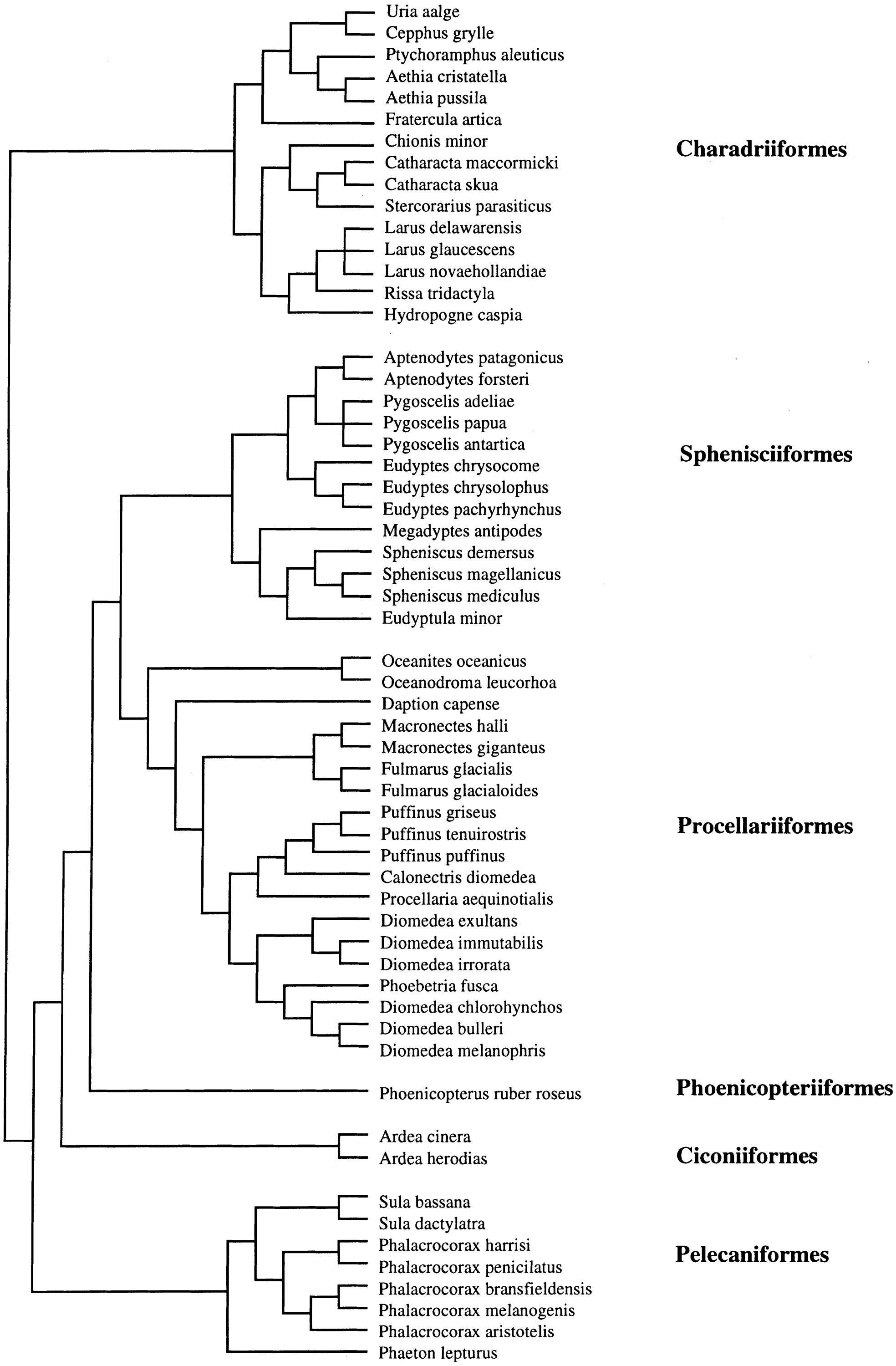
Data on species cannot be considered statistically independent in comparative analysis because similarities can result from either common ancestry or convergent evolution (Harvey and Pagel 1991). A preliminary nested analysis of variance revealed that 69.8% of the variance in divorce rates was accounted for by the family level, showing that the character distribution has a strong component of shared ancestry (see Björklund 1997). Therefore, it was necessary to base comparisons between species on the number of times relations have evolved independently.

We tested whether the pattern of association between divorce rate, a continuous variable, and degree of coloniality, a discrete variable, was evidence for correlated evolutionary change in the two characters using a comparative method based upon generalised least squares (Pagel 1998), and suitable for well-resolved phylogenies. The generalised least squares (GLS) approach uses the phylogeny to specify the pattern of expected phylogenetic associations among species, and calculates the correlation and regression among pairs of traits having controlled for these phylogenetic effects. The correlation was calculated as the covariance between divorce and coloniality divided by the product of the two standard deviations of divorce and coloniality. The association is an estimate of the relationship that held between the two variables as they evolved along the branches of the phylogenetic tree, elsewhere (Pagel 1993) referred to as the "evolutionary regression coefficient". For bifurcating phylogenies the well known independent-contrasts approaches [e.g. Pagel 1992 as implemented in comparative analysis by independent contrasts (CAIC): Purvis and Rambaut 1995] are a subset of the GLS method, and both techniques estimate the same parameters. One advantage of the GLS method when a well resolved phylogeny is to hand is that it does not lose information about the y-axis intercept of the relationship between two variables, making it unnecessary to force regressions through the origin as is done with contrast methods. With respect to the special case of paired-comparisons procedures for the combination of a binary and a continuous variable, the GLS method, unlike other techniques, makes use of all of the information in the data. Further description of the GLS approach can be found in Pagel (1998).

We also analysed the data after categorising divorce rate as a binomial variable (above vs. below the mean on log-transformed data). For these analyses we used the discrete variable method of Pagel (1994). This method uses a continuous-time Markov model to characterize evolutionary changes along each branch of a phylogenetic tree. Two models are fitted to the data, one allowing only for independent evolution, the other allowing for correlated evolution of the two characters. The latter model enables one to ask not only whether the two variables tend to evolve together, but also to ask whether changes in one variable make changes in another more or less likely.

Both the GLS and the discrete variables methods test the hypothesis of correlated evolution using a likelihood ratio test statistic, where $LR = -2\log_e[H_0/H_1]$. In the case of the GLS model H_0 is the null model of no association between the two traits and H_1 is

Fig. 1 Phylogeny of colonial waterbirds



the alternative model allowing for a correlation. The LR statistic tests whether H_1 fits the data better than H_0. The statistic is asymptotically chi-squared distributed with 1 degree of freedom for each correlation that is estimated. The LR statistic for the Discrete model compares the fit of the independent model as H_0 to the fit of the dependent or correlated evolution model as H_1. This test is asymptotically chi-square distributed with 4 degrees of freedom.

We also used the discrete variables method to test the temporal ordering and direction of evolutionary change of the two variables on the phylogeny. The method allows various one degree of freedom tests of whether specified character transitions are significantly different from zero, or from each other. We tested models of evolution in which certain types of transitions are excluded a priori. The fit of a "reduced model" in which a parameter value is constrained is compared to a 'full model in which the parameter is free to vary. Pagel (1994, 1998) gives more information on both kinds of LR tests.

The phylogenetic tree (Fig. 1) is a composite of several phylogenies (O'Hara 1989, Sibley and Ahlquist 1990, Thumser and Karron 1994; Nunn et al. 1996), and branch lengths are taken to be equal.

Results

The raw across-species data showed that species forming large and dense colonies had on average higher divorce rates compared to species forming small or loose aggregations (Fig. 2). The association between divorce rate and the degree of coloniality was confirmed in a phylogenetic context by the generalised least squares approach. The model assuming a correlated evolution of the two characters provided a better fit to the data than the model assuming independent evolution (Table 2). The correlation between divorce and coloniality is 0.418, indicating higher divorce rates amongst colonially nesting birds.

Table 3 shows the results of the discrete variables method when applied to the categorised divorce rate and coloniality data. The results confirm that evolutionary transitions in the two variables are correlated. The probable ancestral states for the two variables (as judged by parsimony) are breeding in large, dense colonies with no mate fidelity. The first variable had a 50% likelihood associate with the two states. However, data from the fossil record (Brodkorb 1963; Feducia (1976); Feducia 1977, 1980) and recent comparative studies on the evolution of coloniality in birds (Rolland et al. 1998) indicate that ancestral species were nesting in large, dense colonies. The second variable had 92% of the likelihood associated with the state of low mate fidelity. We used the discrete model to ask which of these variables changes first during the evolution of loosely colonial species with high mate fidelity (Fig. 3). The rate of evolution from highly colonial to loosely colonial waterbirds but with no change in the background state of no-mate fidelity was significantly different from zero ($\chi^2 = 6.99$, $df = 1$, $P = 0.008$), whereas the transition from no-fidelity to fidelity in the presence of high density was not significant ($\chi^2 = 1.25$, $df = 1$, $P > 0.25$). Mate retention rates do, however, change following the transition to loose coloniality (Fig. 3). Taken together, these results suggest that the evolution of mate fidelity proceeds from the ancestral character states first by a change towards loose coloniality, which in turn makes more likely the evolution of high mate fidelity. In species showing high mate fidelity, the rate of evolution from a low to a high degree of coloniality was significant ($\chi^2 = 12.62$, $df = 1$, $P < 0.001$) but the rate of evolution in the reverse direction was also significant ($\chi^2 = 15.36$, $df = 1$, $P < 0.001$). In summary, we propose the following sequence of events as the most likely scenario for the coupled evolution of divorce and coloniality (Fig. 3). First, a transition occurred from the formation of large, dense colonies to nesting in small and/or loose colonies. Then evolution towards mate fidelity took place, with the preservation of pair-bonds over consecutive seasons. In a third stage, the

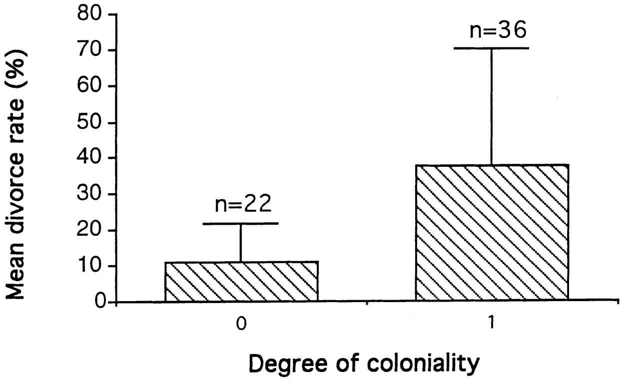


Fig. 2 Mean divorce rate in species with a low degree of coloniality (0) and species with a high degree of coloniality (1)

Table 2 Comparison of likelihood values for models of independent versus dependent evolution of divorce (continuous variable) and degree of coloniality

Model	Likelihood value	
Independent evolution of divorce and coloniality	−109.44	
		Likelihood ratio test = 5.48, $\chi^2 = 10.96$, $df = 1$, $P < 0.001$
Dependent evolution of divorce and coloniality	−103.96	

Table 3 Comparison of likelihood values for models of independent versus dependent evolution of divorce (discrete variable) and degree of coloniality

Model	Likelihood value	
Independent evolution of divorce and coloniality	−73.15	
		Likelihood ratio test = 5.62, $\chi^2 = 11.24$, $df = 4$, $P < 0.01$
Dependent evolution of divorce and coloniality	−67.53	

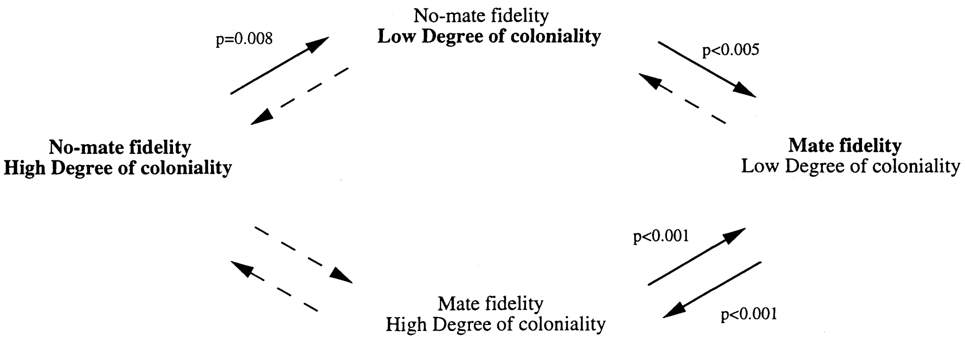


Fig. 3 Flow diagram tracing the joint evolution of mate fidelity and coloniality in waterbirds

degree of coloniality varied again without any noticeable effect on mate fidelity.

Discussion

Several microevolutionary studies (see Table 1 for references) have concentrated on the determinants of social fidelity in colonial waterbirds in current environments where the various processes shaping the interactions between mates can be observed and measured directly. The use of the general method of comparative analysis (Pagel 1994, 1998) complements these studies by both testing for an association between divorce and the degree of coloniality, and reconstructing the historical patterns of character origin and diversification.

Our analysis of correlated evolutionary change provides evidence for a positive association between divorce rate and the degree of coloniality in waterbirds. Overall, species showing a high degree of coloniality tend to have weak or no mate fidelity whereas species with a low degree of coloniality tend to be mate-faithful. These results provide some support for the better option hypothesis, as mate switching appears to be favoured in species nesting in large, dense colonies where public information on the quality of alternative partners is available. An alternative explanation can also be considered. Our analysis indicates that the probable ancestral state corresponds to species forming large, dense colonies and showing low or no mate fidelity. This situation is typical of ancient lineages such as flamingos (Cézilly and Johnson 1995) or cormorants (Boekelheide and Ainley 1989; Aebischer et al. 1995). These species typically breed in unstable habitats where they build rudimentary nests, and show little, if any, territorial defense. Tests of specific directional hypotheses reveal that the evolution from large, dense colonies towards colonies smaller in size and density has preceeded the evolution towards mate fidelity. This conforms to the idea that breeding space limitation became less important as colonial waterbirds started nesting in more stable habitats (Siegel-Causey and Kharitonov 1990). Nesting in stable habitats may have provided an opportunity for the evolution of breeding site fidelity. Contrary to species living in unstable habitats, species breeding in stable habitats tend to build more elaborated nests that they may have advantage to reuse over consecutive breeding seasons. They also show a higher degree of territorial defense. Mate fidelity may then have evolved simply as a by-product of site fidelity in males and females (Morse and Kress 1984; Cuthbert 1985; Cézilly and Johnson 1995).

On the other hand, site fidelity may have evolved precisely because it enhanced the probability to meet again with the same mate through successive breeding seasons. In this second case, keeping the same mate through consecutive breeding attempts must confer some benefits in terms of breeding success. Although several studies have shown that mate-retention increased breeding success in some colonial waterbirds (e.g. Williams and Rodwell 1992; Thibault 1994), some studies have found no such evidence in other species (e.g. Reilly and Cullen 1981; Emslie et al. 1992; Williams and Rodwell 1992). Therefore it is unlikely that site fidelity evolved because of benefits from mate fidelity. Rather, once colonial waterbirds have started nesting in more stable habitats, colony size may vary according to various factors, such as the availability of food resources or predation risk (Wittenberger and Hunt 1985; Siegel-Causey and Kharitonov 1990) without any influence on site fidelity, and hence mate fidelity. Although mate fidelity is associated with the degree of coloniality among waterbirds, this association is thus likely to be influenced by the relationship between mate fidelity and habitat stability. Therefore, a more direct test of the hypothesis could consist in studying the relationship between divorce rate and colony density at the intraspecific level.

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