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Animal behaviour

Boldness predicts divorce rates in wandering albatrosses (*Diomedea exulans*)

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Personality predicts divorce rates in humans, yet how personality traits affect divorce in wild animals remains largely unknown. In a male-skewed population of wandering albatross (*Diomedea exulans*), we showed that personality predicts divorce; shyer males exhibited higher divorce rates than bolder males but no such relationship was found in females. We propose that divorce may be caused by the intrusion of male competitors and shyer males divorce more often because of their avoidance of territorial aggression, while females have easier access to mates regardless of their personality. Thus, personality may have important implications for the dynamics of social relationships.

1. Introduction

Consistent individual-level behavioural differences, i.e. 'personality', should affect pair-bond dynamics inherently, as a diverse range of activities, such as territory defence and parental care, rely on the behavioural compatibility of two partners [1–4]. Personality may affect not only the formation but also the maintenance of existing pair-bonds in monogamous species. Indeed, as partnership relies on interactive negotiations over resource allocation to parental care and considering that reproduction is costly [1], conflicts may arise and, depending on personality traits of partners, result in divorce. As a driver of both pair-bond formation and divorce, personality may have implications for both annual and lifetime reproductive success of individuals ([5–8]). Although a link between personality and divorce has been established in humans [9,10], lack of long-term empirical data on both personality and divorce rates [11–13] has so far prevented us from making this link in wild animal populations.

Personality is often measured along a shy-bold axis linked to individual risk-taking tendency with bolder individuals being more likely to take risks and shyer individuals showing greater behavioural plasticity to avoid risks [14–17]. This shy-bold axis is expected to align with the slow-fast continuum of life-history strategies defined by life-history trade-offs between survival and reproduction [18–22]. Specifically, bolder individuals should risk reproducing at the expense of survival, whereas shyer individuals should sometimes skip breeding to preserve their body condition and future reproductive opportunities as a conservative strategy. Divorce may thus be adaptive for shyer individuals to optimize their lifetime reproductive success when they decide to skip breeding while their partners focus on current reproduction (i.e. incompatibility in figure 1*a*). Bolder individuals, on the other hand, may

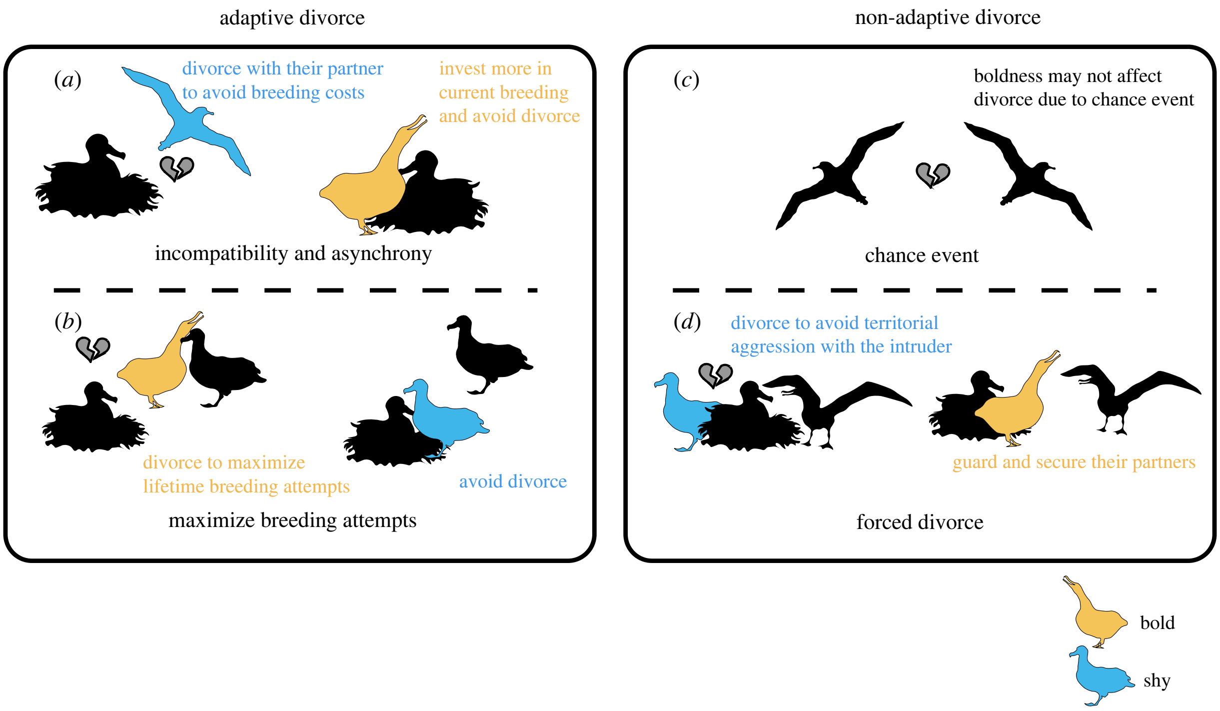

Figure 1. Different hypotheses linking personality and divorce in monogamous species. Adaptive divorce (*a*,*b*) can arise from partner (*a*) incompatibility or asynchrony, or (*b*) maximization of breeding attempts. For example, (*a*) shyer individuals (blue) may postpone or skip breeding as a conservative strategy, which may result in partner incompatibility or asynchrony and ultimately divorce (represented here by a broken heart). Bolder individuals (yellow), by largely and consistently investing in current reproduction, may avoid divorce. If divorce allows maximizing lifetime breeding attempts (*b*), bolder individuals may divorce more often. Non-adaptive divorce (*c*,*d*) can result from (*c*) chance events, or (*d*) eviction from a same-sex intruder, which is referred to as 'forced-divorce'. In (*c*), boldness may not affect divorce but in the case of forced divorce (*d*), shyer individuals may avoid territorial aggression from an intruder and be forced to divorce, whereas aggressive bolder individuals may guard their partner and avoid divorce.

consistently allocate resources to their current reproduction, following a fast life-history strategy, and thus divorce less often (figure 1*a*). Adaptive divorce may also happen in bolder individuals if it allows spreading reproductive effort over different partners and maximizing lifetime breeding attempts (figure 1*b*).

Adaptive divorce may be less common than previously thought [23], and several alternative non-adaptive causes of divorce also exist with potential links to personality. Chance events, such as accidental loss of contact between partners, are unlikely to be affected by personality (figure 1*c*). Divorce can also occur when a competitor evicts one partner to gain access to the other partner. In this form of non-adaptive divorce, referred to as 'forced-divorce' [13], personality has straightforward implications. Bolder individuals may be more likely to guard their partners against competitors, whereas shyer individuals, who tend to avoid territorial aggression, should be more vulnerable to forced divorce (figure 1*d*).

Here, based on 54 years of individual-based monitoring data and 10 years of personality measurements, we investigated whether personality affects divorce rates in a long-lived monogamous seabird, the wandering albatross (*Diomedea exulans*). Personality was measured on 1942 adults by assessing boldness, i.e. a score reflecting an individual's responsiveness towards human approaches during incubation [24] (see Methods). In this population, divorce is probably non-adaptive as it does not improve breeding success for either sex, however, remaining unpaired reduces lifetime reproductive success for males [25]. This population is male-skewed [26], with more males available for mating than females, which should increase competition between males and the likelihood of forced divorce events [25].

2. Methods

(a) Study species and system

Wandering albatrosses are socially monogamous and form lifelong partnerships [27]. They are generally regarded as biennial breeders because of their long chick-rearing period (up to 280 days), and most individuals take a sabbatical year at sea after each breeding attempt [28]. A long-term monitoring programme has taken place on a wandering albatross population at Possession Island (46°24′ S, 51°46′ E), in the Crozet archipelago of the Southern Indian Ocean since 1959. Observations of breeding birds and partner identities occurred from January to February (3–4 visits per nest) starting immediately after egg-laying, and all chicks were ringed with uniquely numbered stainless steel rings in September and October before fledging [12]. Incidental fishery bycatch, as a major threat affecting the survival of wandering albatrosses, has caused sex-biased mortality rates since 1970 s resulting in an accumulated high proportion of widowed males in this population and a male-skewed operational sex ratio [12,26,29].

(b) Personality measurements

Boldness has been measured in incubating individual birds since 2008. Boldness corresponds to the behavioural response of the bird towards an approaching human at 5 m from the nest [30]. To avoid the confounding effects of mate behaviours, tests were carried out when only one partner was present at the nest. The behavioural response was classified on an ordinal scale from zero to five: 0 = no response; 1 = bird lifts the head; 2 = bird raises up onto tarsus; 3 = bird vocalizes; 4 = bird stands up; 5 = bird leaves the nest which is an extremely rare event [24,30]. In this study, we used corrected boldness scores extracted from the work of Patrick *et al.* [24]. In wandering albatrosses, our

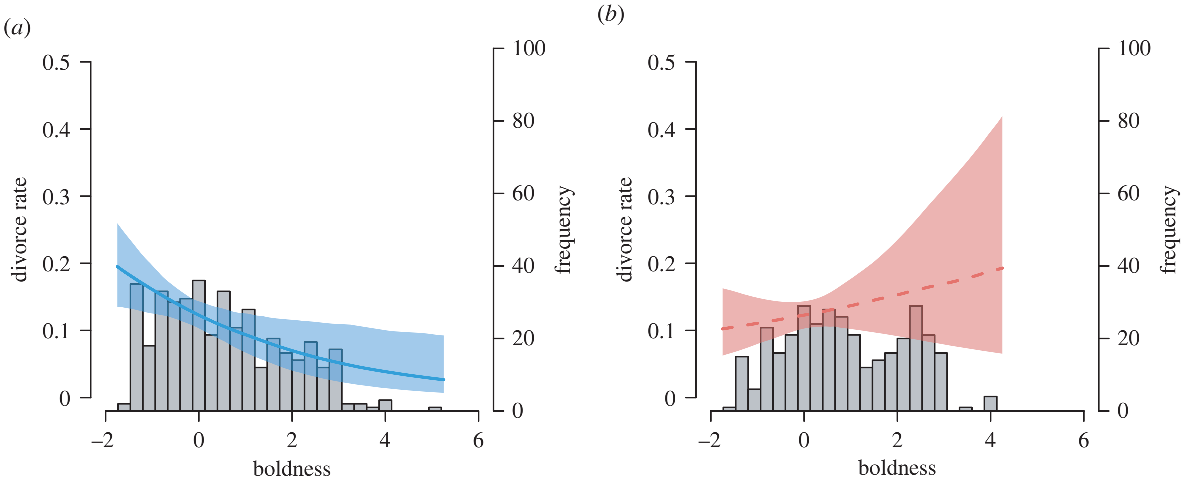

Figure 2. Relationships between individual boldness score (personality) and divorce rates in (*a*) male ($p < 0.01$, significant) and (*b*) female ($p = 0.46$, not significant) wandering albatrosses. Boldness scores were standardized (mean = 0, s.d. = 1). Lines show the GLMM-based predictions (see Methods and the electronic supplementary material, appendix S1: table S1 for a full model list) and shaded areas show the ±95% confidence intervals. Grey bars show the frequency distribution of boldness scores.

proxy of boldness has been shown to be highly repeatable and heritable [24]. There is also little evidence that boldness changes with age and environmental conditions [30], which supports the use of boldness scores as proxies of personality across the lifetime of wandering albatrosses.

(c) Analysis

We constructed a dataset containing each pair-bond relationship (female: 490; male: 622) and its fate (1 = divorce, or not = 0). Because pair-bond disruption can happen either through divorce or widowhood, we assigned divorce to both partners simultaneously when at least one of them was observed breeding with a new partner, while both partners were still alive. Divorce was modelled as a binary response variable with a logit link function using a generalized linear mixed model (GLMM). Individual boldness score was included as an explanatory variable along with its interaction with sex to explicitly test sex-specific effect of boldness on divorce rate. The year of the pair-bond disruption was included as a random effect to control for annual variability and environmental disturbance. We included: (i) breeding experience, (ii) previous breeding success, and (iii) pair-bond duration as controlling variables which were previously found to affect divorce rates [25]. Breeding experience was measured at an individual level as the total number of years an individual was observed as a breeder (either succeed or failed) in the colony up to the current time point. Breeding experience and its quadratic term were both included in the model to account for changes in individual reproductive performance with age [31]. We used breeding experience instead of age as a predictor because the age of some individuals was unknown, whereas we had precise information on breeding experience for a larger number of individuals. Breeding experience and age are also highly correlated in this population [25]. Previous breeding success was calculated for each pair-bond relationship. We included both the long-term breeding success, defined as the averaged breeding success of a pair across the entire pair-bond duration, and the short-term breeding success, defined as the very last breeding attempt made by the pair prior to the pair-bond disruption. Pair-bond duration, defined as the period of time that partners spend together as a pair, has been shown to affect behavioural coordination and compatibility between partners to successfully raise offspring (the ‘mate familiarity hypothesis’) [32,33]. Thus, the number of breeding attempts made with a particular partner was included to control for the effects of the pair-bond duration of the relationship. All continuous variables were scaled (mean = 0 and standard deviation = 1) prior to analyses. Models were analysed in R [34] using the lme4 R package [35]. A series of models were built based on combinations of explanatory variables. Model selection (electronic supplementary material, appendix S1: table S1) was based on Akaike’s information criterion using the MuMIn package in R [36]. We used the best-supported model to calculate parameter estimates.

3. Results

Our analyses revealed a sex-specific effect of personality on divorce rates in wandering albatrosses (see the electronic supplementary material, appendix S1: table S1 for the full list of candidate models tested). There were 71 divorce events out of 490 records in females and 88 divorce events out of 622 in males. The average divorce rate was 0.13 (s.e. = 0.01) and 0.12 (s.e. = 0.01) for females and males, respectively. Divorce rates were influenced by boldness, pair-bond duration, and breeding experience. When controlling for breeding experience and number of breeding attempts of a pair, we found a negative relationship between divorce rates and boldness in males (estimate: −0.33, s.e. = 0.13, $p < 0.01$, figure 2*a*), but not in females (estimate: 0.10, s.e. = 0.14, $p = 0.46$, figure 2*b*). Specifically, shyer males had higher divorce rates than bolder males.

Both breeding experience and number of breeding attempts with a partner affected divorce rates linearly. Divorce rates of the focal individual decreased as the number of breeding attempts with a partner increased (estimate: −0.71, s.e. = 0.12, $p < 0.001$) and were higher for more experienced individuals (estimate: 0.35, s.e. = 0.10, $p < 0.001$).

4. Discussion

Our findings demonstrated that individual-level behavioural differences affect divorce in a wild monogamous seabird population. The higher divorce rates of shyer males are in line with the forced divorce hypothesis (figure 1*d*). Wandering albatrosses show elaborate courtship processes, including complex visual, vocal and behavioural displays [37–39]. These displays are crucial to establish compatibility between partners and forge long-term pair-bonds. With many available males competing for mates, male intrusions are very likely during courtship [26,40,41]. Therefore, the higher divorce rates of shyer males support the hypothesis that shyer males tend to avoid risks of guarding their current pair-bond and engaging in antagonistic interactions with intruders (figure 1*d*). In this male-skewed population, personality may play a lesser role in female divorce rates, as they have access to mating opportunities regardless of their personality and have never been observed actively seeking extra-pair mating opportunities [27].

An alternative, and non-exclusive, hypothesis to explain the link between boldness and divorce is that shyer males may either skip breeding or delay their arrival at the colony to recover from the last breeding attempt, which may lead to divorce between partners (asynchrony hypothesis in figure 1*a*). In slow-breeding seabirds like the wandering albatross, breeding is highly energy-consuming and body condition predicts reproductive decisions and performance [42–44]. Not all individuals are able to replenish their body condition in one sabbatical year, causing delay or skipped breeding in the next breeding season [45]. Therefore, shyer individuals may skip breeding more often, as they exhibit higher plasticity in breeding decisions driven by their body condition. In this male-skewed population, single females can re-mate quickly, whereas it may take up to 4.3 years for a male to find a new mate [25]. Therefore, shyer females skipping breeding may still be able to mate with their original mate, which can potentially explain why shyer females do not have higher divorce rates as shyer males do. Nevertheless, given that the mating season is long, and that partners display for roughly a month before breeding providing sufficient fault tolerance of arrival time [41], late arrival may not be the main reason for permanent divorce in this population. Combined with observations of temporary divorce in female wandering albatrosses [46], i.e. breeding with another transient partner while their long-term partner skips breeding, permanent divorce is unlikely to be driven by the asynchrony between partners.

By shaping pair-bond dynamics, personality traits may undergo selective pressures, as pair-bond disruptions can affect individual lifetime reproductive success. Considering that operational sex ratio (OSR) can also mediate pair-bond dynamics [47], the selective pressures of personality traits may also depend on the OSR of a population. In human populations, personality traits predicting long-term partnerships are selected when females are the limiting sex, whereas personality traits associated with lower relationship stability are selected when males are limiting [48]. In non-human populations, several personality traits affect mating and parenting-related behaviours [49–51], and OSR-driven selective pressure on personality may also be expected. In our study population, breeding success does not differ between shyer and bolder males in their early adulthood, but bolder males are known to have higher reproductive success in their late adulthood [30]. This reproductive advantage of bolder males may be offset by their higher survival risks, especially since the risk-proneness makes bolder individuals more susceptible to mortality factors. A comparison of lifetime reproductive success between individuals expressing different personalities would be required to fully assess whether personality is under selection.

In conclusion, we present, to our knowledge, the first evidence that individual personality predicts divorce rates of a wild species. Divorce in wandering albatross is probably non-adaptive, but testing the impact of personality in adaptive divorce (figure 1) would allow a better understanding of the role of personality in driving pair-bond dynamics and mating strategies. From an evolutionary point of view, understanding the selective pressures acting on personality is of great interest, especially if different personality types lead to divergent demographic consequences.

Ethics. Licences and permissions were granted by the Ethic Committee of Institut Polaire Francais (IPEV) and by the Préfet of Terres australes et antarctiques francaises (TAAF) after advice from the Comité de l'Environnement Polaire (CEP).

Data accessibility. The data are provided in the electronic supplementary material [52].

Authors' contributions. R.S.: conceptualization, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; J.V.d.W.: methodology, writing—review and editing; S.C.P.: conceptualization, data curation, funding acquisition, methodology, writing—review and editing; C.B.: data curation, writing—review and editing; H.W.: data curation, writing—review and editing; K.D.: data curation, writing—review and editing; S.J.: conceptualization, funding acquisition, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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