

Boldness predicts divorce rates in wandering albatrosses

(Diomedea exulans)

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Abstract

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 due to 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.

Keywords: behavioural syndromes; boldness; mate competition; monogamy; sex bias; social networks;

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 optimise their lifetime reproductive success when they decide to skip breeding while their partners focusing on current reproduction (i.e., incompatibility in Fig. 1a). Bolder individuals, on the other hand, may consistently allocate resources to their current reproduction, following a fast life-history strategy, and thus divorce less often (Fig. 1a). Adaptive divorce may also happen in bolder individuals if it allows spreading reproductive effort over different partners and maximise lifetime breeding attempts (Fig. 1b).

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

42 accidental loss of contact between partners, are unlikely to be affected by personality (Fig. 1c).
43 Divorce can also occur when a competitor evicts one partner to gain access to the other part-
44 ner. In this form of non-adaptive divorce, referred to as “forced-divorce” [13], personality has
45 straightforward implications. Bolder individuals may be more likely to guard their partners against
46 competitors, whereas shyer individuals, who tend to avoid territorial aggression, should be more
47 vulnerable to forced divorce (Fig. 1d).
48 Here, based on 54 years of individual-based monitoring data and 10 years of personality mea-
49 surements, we investigated whether personality affects divorce rates in a long-lived monogamous
50 seabird, the wandering albatross (*Diomedea exulans*). Personality was measured on 1,942 adults
51 by assessing boldness, i.e., a score reflecting an individual’s responsiveness towards human ap-
52 proaches during incubation [24] (see Methods). In this population, divorce is likely non-adaptive
53 as it does not improve breeding success for either sex, however, remaining unpaired reduces life-
54 time reproductive success for males [25]. This population is male-skewed [26], with more males
55 available for mating than females, which should increase competition between males and the like-
56 lihood of forced divorce events [25].

57 **2 Methods**

58 **2.1 Study species and system**

59 Wandering albatrosses are socially monogamous and form lifelong partnerships [27]. They are
60 generally regarded as biennial breeders because of their long chick-rearing period (up to 280 days),
61 and most individuals take a sabbatical year at sea after each breeding attempt [28]. A long-term
62 monitoring program has taken place on a wandering albatross population at Possession Island
63 (46°24’S 51°46’E), in the Crozet archipelago of the Southern Indian Ocean since 1959. Obser-
64 vations of breeding birds and partner identities occurred from January to February (3–4 visits per
65 nest) starting immediately after egg-laying and all chicks were ringed with uniquely numbered
66 stainless steel rings in September and October before fledging [12]. Incidental fishery bycatch,

67 as a major threat affecting the survival of wandering albatrosses, has caused sex-biased mortality
68 rates since 1970s resulting in an accumulated high proportion of widowed males in this population
69 and a male-skewed operational sex-ratio [12, 26, 29].
70 [30, 31].

71 **2.2 Personality measurements**

72 Boldness has been measured in incubating individual birds since 2008. Boldness corresponds to
73 the behavioural response of the bird towards an approaching human at 5 meters from the nest [32].
74 To avoid the confounding effects of mate behaviours, tests were carried out when only one partner
75 was present at the nest. The behavioural response was classified on an ordinal scale from zero to
76 five: 0 = no response; 1 = bird lifts the head; 2 = bird raises up onto tarsus; 3 = bird vocalises;
77 4 = bird stands up; 5 = bird leaves the nest which is an extremely rare event [24, 32]. In this
78 study, we used corrected boldness scores extracted from the work of Patrick, Charmantier, and
79 Weimerskirch [24]. In wandering albatrosses, our proxy of boldness has been shown to be highly
80 repeatable and heritable [24]. There is also little evidence that boldness changes with age and
81 environmental conditions [32], which supports the use of boldness scores as proxies of personality
82 across the lifetime of wandering albatrosses.

83 **2.3 Analysis**

84 We built a data set containing each pair-bond relationships (female: 490; male: 622) and its fate
85 (1 = divorce, or not = 0). Divorce was assigned to both partners simultaneously when at least one
86 of them was bred with a new partner, while both of them were still alive. Divorce was modeled
87 as a binary response variable with a logit link function using a Generalised Linear Mixed Model
88 (GLMM). Individual boldness score was included as an explanatory variable and its interaction
89 with sex to explicitly test sex-specific effect of boldness on divorce rate. The year of the pair-bond
90 disruption was included as a random effect to control for annual variability and environmental
91 disturbance. Controlling variables include (1) breeding experience, (2) previous breeding success,

92 and (3) pair-bond duration which are expected to affect divorce rate [25]. Breeding experience was
93 measured as the total number of breeding attempts either failure or success made by an individual at
94 the current time point. Breeding experience and its quadratic term were both included in the model
95 to account for changes of individual reproductive performance with age [33]. We used breeding
96 experience instead of age as a predictor because the age of some individuals was unknown, whereas
97 we had precise information on breeding experience for a larger number of individuals. Breeding
98 experience and age are also highly correlated in this population [25]. We included both the long-
99 term breeding success defined as the averaged breeding success of a pair across the entire pair-bond
100 duration and the short-term breeding success defined as the very last breeding attempt made by the
101 pair prior to pair-bond disruption. Pair-bond duration, defined as the period of time that partners
102 spend together as a pair, has been shown to affect behavioural coordination and compatibility
103 between partners to successfully raise offspring (the ‘mate familiarity hypothesis’) [34, 35]. Thus,
104 the number of breeding attempts made with a particular partner was included to control for the
105 effects of the pair-bond duration of the relationship. All continuous variables were scaled (mean
106 = 0 and standard deviation = 1) prior to analyses. Models were analysed in R [36] using the lme4
107 R package [37]. A series of models were built based on combinations of explanatory variables.
108 Model selection (Appendix S1: Table S1) was based on Akaike’s Information Criterion (AIC)
109 using the MuMIn package in R [38]. We used the best supported model to calculate parameter
110 estimates.

111 **3 Results**

112 Our analyses revealed a sex-specific effect of personality on divorce rates in wandering albatrosses
113 (see Appendix S1: Table S1 for the full list of candidate models tested). There were 71 divorce
114 events out of 490 records in females and 88 divorce events out of 622 in males. The average divorce
115 rate was 0.13 (SE = 0.01) and 0.12 (SE = 0.01) for females and males, respectively. Divorce rates
116 were influenced by boldness, pair-bond duration, and breeding experience. When controlling for

117 breeding experience and number of breeding attempts of a pair, we found a negative relationship
118 between divorce rates and boldness in males (estimate: -0.33 , $SE = 0.13$, $P < 0.01$, Fig. 2a),
119 but not in females (estimate: 0.10 , $SE = 0.14$, $P = 0.46$, Fig. 2b). Specifically, shyer males had
120 higher divorce rates than bolder males.
121 Both breeding experience and number of breeding attempts with a partner affected divorce rates
122 linearly. Divorce rates of the focal individual decreased as the number of breeding attempts with a
123 partner increased (estimate: -0.71 , $SE = 0.12$, $P < 0.001$), and were higher for more experienced
124 individuals (estimate: 0.35 , $SE = 0.10$, $P < 0.001$).

125 **4 Discussion**

126 Our findings demonstrated that individual-level behavioural differences affect divorce in a wild
127 monogamous seabird population. The higher divorce rates of shyer males are in line with the
128 forced divorce hypothesis (Fig. 1d). Wandering albatrosses show elaborate courtship processes,
129 including complex visual, vocal, and behavioural displays [39–41]. These displays are crucial
130 to establish compatibility between partners and forge long-term pair-bonds. With many available
131 males competing for mates, male intrusions are very likely during courtship [26, 42, 43]. There-
132 fore, the higher divorce rates of shyer males support the hypothesis that shyer males tend to avoid
133 risks of guarding their current pair-bond and engaging in antagonistic interactions with intruders
134 (Fig. 1d). In this male-skewed population, personality may play a lesser role in female divorce
135 rates, as they have access to mating opportunities regardless of their personality and have never
136 been observed actively seeking extra-pair mating opportunities [27].

137 An alternative, and non-exclusive, hypothesis to explain the link between boldness and divorce is
138 that shyer males may either skip breeding or delay their arrival at the colony to recover from the last
139 breeding attempt, which may lead to divorce between partners (asynchrony hypothesis in Fig. 1a).
140 In slow-breeding seabirds like the wandering albatross, breeding is highly energy-consuming and
141 body condition predicts reproductive decisions and performance [44–46]. Not all individuals are

142 able to replenish their body condition in one sabbatical year, causing delay or skipped breeding in
143 the next breeding season [31]. Therefore, shy individuals may skip breeding more often, as they
144 exhibit higher plasticity in breeding decisions driven by their body condition. In this male-skewed
145 population, single females can re-mate quickly, whereas it may take up to 4.3 years for a male to
146 find a new mate [25]. Therefore, shy females skipping breeding may still be able to mate with
147 their original mate, which can potentially explain why shy females do not have higher divorce
148 rates as shy males do. Nevertheless, given that the mating season is long, and that partners
149 display for roughly a month before breeding providing sufficient fault tolerance of arrival time [43],
150 late arrival may not be the main reason for permanent divorce in this population. Combined with
151 observations of temporary divorce in female wandering albatrosses [47], i.e., breeding with another
152 transient partner while their long-term partner skips breeding, permanent divorce is unlikely to be
153 driven by the asynchrony between partners.

154 By shaping pair-bond dynamics, personality traits may undergo selective pressures, as pair-bond
155 disruptions can affect individual lifetime reproductive success. Considering that Operational Sex
156 Ratio (OSR) can also mediate pair-bond dynamics [48], the selective pressures of personality traits
157 may also depend on the OSR of a population. In human populations, personality traits predicting
158 long-term partnerships are selected when females are the limiting sex, whereas personality traits
159 associated with lower relationship stability are selected when males are limiting [49]. In non-
160 human populations, several personality traits affect mating and parenting-related behaviours [50–
161 52], and OSR-driven selective pressure on personality may also be expected. In our study popula-
162 tion, breeding success does not differ between shy and bolder males in their early adulthood, but
163 bolder males are known to have higher reproductive success in their late adulthood [32]. This re-
164 productive advantage of bolder males may be offset by their higher survival risks, especially since
165 the risk-proneness makes bolder individuals more susceptible to mortality factors. A comparison
166 of lifetime reproductive success between individuals expressing different personalities would be
167 required to fully assess whether personality is under selection.

168 In conclusion, we present the first evidence that individual personality predicts divorce rates of a

169 wild species. Divorce in wandering albatross is likely non-adaptive, but testing the impact of per-
170 sonality in adaptive divorce (Fig. 1) would allow a better understanding of the role of personality
171 in driving pair-bond dynamics and mating strategies. From an evolutionary point of view, under-
172 standing the selective pressures acting on personality is of great interest, especially if different
173 personality types lead to divergent demographic consequences.

174 **5 Figure legend**

175 **Figure 1.** Different hypotheses linking personality and divorce in monogamous species. Adaptive
176 divorce (left panel) can arise from partner (a) incompatibility or asynchrony or (b) maximisation
177 of breeding attempts. For example, (a) shyer individuals (blue) may postpone or skip breeding as
178 a conservative strategy, which may result in partner incompatibility or asynchrony and ultimately
179 divorce (represented here by a broken heart). Bolder individuals (yellow), by largely and consis-
180 tently investing in current reproduction, may avoid divorce. If divorce allows maximising lifetime
181 breeding attempts (b), bolder individuals may divorce more often. Non-adaptive divorce (right
182 panel) can result from (c) chance events or (d) eviction from a same-sex intruder, which is referred
183 to as “forced-divorce”. In (c), boldness may not affect divorce but in the case of forced divorce
184 (d), shyer individuals may avoid territorial aggression from an intruder and be forced to divorce,
185 whereas aggressive bolder individuals may guard their partner and avoid divorce.

186 **Figure 2.** Relationships between individual boldness score (personality) and divorce rates in (a)
187 male ($P < 0.01$, significant) and (b) female ($P = 0.46$, not significant) wandering albatrosses.
188 Boldness scores were standardized (mean = 0, sd = 1). Lines show the GLMM-based predic-
189 tions (see Methods and Appendix S1: Table S1 for a full model list) and shaded areas show the
190 $\pm 95\%$ confidence intervals. The relationship between divorce rate and boldness in females is non-
191 significant, but is shown for illustrative purposes only. Gray bars show the frequency distribution
192 of boldness scores.

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202 **7 Author contributions**

203 R.S., S.P. and S.J. conceived the study. R.S., S.P. and J.V.W developed methodology. R.S., carried
204 out the formal analyses, results visualization. R.S., S.J, S.P. and J.V.W. interpreted the results.
205 S.P., H.W., C.B. and K.D. led the wandering albatross monitoring program and provided the data.
206 S.J. and S.P. secured funding. R.S., S.J, and J.V.W. led the writing of the manuscript. All authors
207 contributed significantly to revising the manuscript.

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210 **9 Data accessibility**

211 Data is available as electronic supplementary material.

212 **10 Conflict of interest declaration**

213 We declare we have no competing interest.

214 **11 Ethics statement**

215 Licences and permissions were granted by the Ethic Committee of Institut Polaire Francais (IPEV)
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