

# Ecology of Pairbond Stability

Dr Geoff Kushnick

The Australian National University

Now Published:

Kushnick G (2016) Ecology of pairbond stability. In Shackelford T, Weekes-Shackelford V (eds.), *Encyclopedia of evolutionary psychological science* (pp.1-7). NY: Springer.

To appear in Shackelford & Weekes-Shackelford, eds. (2018) *Encyclopedia of Evolutionary Psychological Science*

**SYNONYMS:** Environmental Factors Associated with Marital Harmony

**DEFINITION:** The study of physical and social environmental factors influencing pairbond stability and dissolution.

## 1. Introduction

Humans are a pairbonding species, and this is reflected in our behaviour and our physiology (Quinlan 2008). While their form and duration varies, pairbonds exist in all human societies—and there are very few, if any, exceptions to this rule. To understand the stability of pairbonds it is useful to look at the contexts under which they are unstable, to examine the factors that increase the probability of divorce or dissolution. These factors have been well studied by scholars in sociology, psychology, anthropology, medicine, and law. Despite this, the *ecological* factors driving pairbond stability and divorce have received much less attention in humans as they have in studies of other pairbonding species, like birds.

This entry will provide a selective and brief account of: (1) the behavioral ecological approach to pairbond stability in humans; (2) mate desertion theory, the primary theoretical approach used in studies of human pairbonding, and empirical tests of the idea; and, (3) studies that have gone beyond the limitations of mate desertion theory.

## 2. Main Text

### 2.1. Behavioral Ecology and Pairbond Stability

Human behavioral ecology is the study of human behavior in evolutionary and ecological context. Under the assumptions of this framework, humans are viewed as actors whose behaviour is shaped by genetic and cultural evolutionary mechanisms to maximize inclusive fitness given the constraints of prevailing ecological conditions. Adopting the wording of Winterhalder and Smith (2000), a typical HBE hypothesis might take the following form: in context X, stay in a pairbond because it maximizes inclusive fitness; in context Y, leave an existing pairbond because it maximizes inclusive fitness.

These hypotheses are often derived from mathematically or graphically formulated optimality models. When the payoffs are frequency-dependent (i.e., one actor's payoff depends on what the other actors are doing), as is often the case with pairbonding, game theory provides the best-fitting analytical tools. The idea of an evolutionarily stable strategy (ESS) comes from this body of theory, and can be defined as "a strategy such that, if all members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection" (Maynard Smith, 1982, p. 10).

Pairbonds can dissolve via divorce, abandonment, or death. The first two causes of dissolution should occur when one or both in the pair can increase their fitness by doing so, for

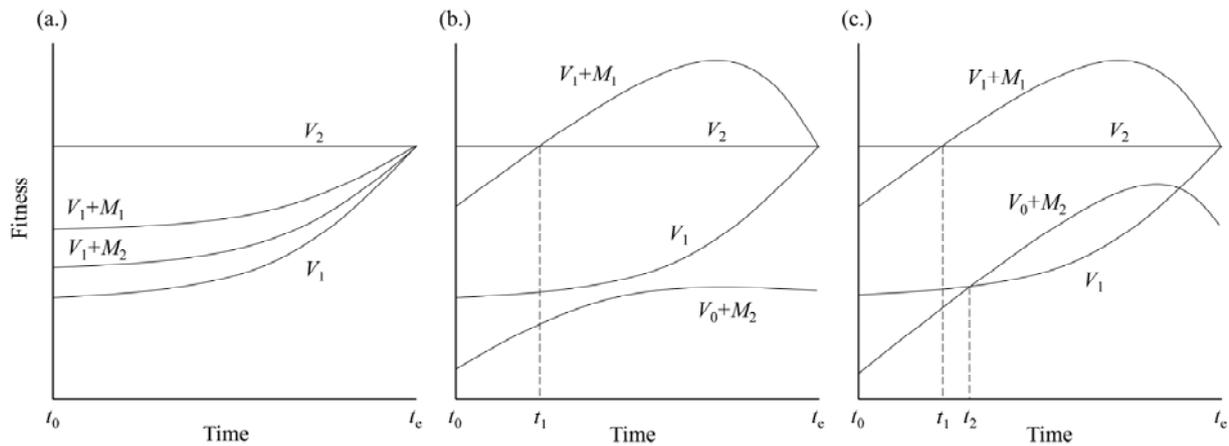
instance, by having a reasonable probability of finding a better mate. The third cause, mortality, is out of the actors' control (except, perhaps, in the case of spousal homicide). Despite these fundamental differences, both should be influenced by ecological conditions.

### 2.2. Mate Desertion Theory

Maynard Smith (1977, 1982) can be credited for bringing game theory to bear on the problem of mate desertion. In his models, the decision to stay or desert depends on the *frequency-dependent* fitness payoffs for staying (parenting effort) as traded off against a *fixed* payoff for seeking additional mating opportunity (mating effort). While the prospective nature of the models improves on existing ones that viewed past investments as reasonable drivers of future ones, they are now viewed as having a serious shortcoming (Houston, Szekely, & McNamara, 2013). The mating benefits of desertion should be a frequency-dependent, rather than fixed, function of how many opposite-sex individuals have left their own pairing in favor of the mating pool. More recent models of mate desertion account for this.

The major conclusions drawn from these models are as follows. First, mate desertion will occur when the fitness benefits of seeking additional mates outweighs the decrease in offspring survival caused by reducing the number of individuals providing parental care. Second, desertion by none, both, or one partner can be an evolutionary stable strategy. This is illustrated graphically in Figure 1 using examples from Lazarus (1990). In these illustrations, the fitness accrued between the start ( $t_0$ ) and end ( $t_e$ ) of the period of parental care for biparental care is  $V_2$ , uniparental care is  $V_1$ , and no care is  $V_0$ . The fitness accrued in searching for another mate is  $M_1$  for the partner with the higher, and  $M_2$  for the partner with the lower, marginal gains. In (a.), neither partner deserts because  $V_1+M_1 < V_2$  and  $V_1+M_2 < V_2$ . In both (b.) and (c.), the first partner deserts at  $t_1$  because  $V_1+M_1 > V_2$ . In (b.) the second partner does not desert because  $V_0+M_2 < V_1$ . In (c.) the second partner deserts the offspring at  $t_2$  because  $V_0+M_2 > V_1$ .

Harpending and Draper (1986) argued for the application of mate desertion theory to the problem of human pairbond stability, identifying specific aspects of the socioeconomic environment that shape the payoffs. They pointed to fertility rates as a measure of the potential payoffs for mating, and care-independent child mortality rates as a measure of the potential payoffs for fathering. In relatively good environments, where increases in paternal care lead to increases in offspring survivorship, more stable pairbonds are expected compared to relatively bad



**Figure 2.** Illustrations adapted from Lazarus’s (1990) model of mate desertion, depicting scenarios where: (a.) neither partner deserts, (b.) one partner deserts, and (c.) both partners desert. The following parameters describe fitness payoffs:  $V_2$  is the payoff for biparental care;  $V_1$  for uniparental care;  $V_0$  for no care;  $M_1$  is the payoff to looking for an additional mate for partner 1; and,  $M_2$  is the payoff to looking for an additional mate for partner 2. The labels on the time axis describe the following:  $t_0$  is the start and  $t_c$  is the end of the period of parental care; and,  $t_1$  and  $t_2$  are the timings of desertion for partner 1 and 2.

environments where paternal care is unlikely to increase offspring survivorship. The focus on payoffs to males was due in large part to males being the ones with higher marginal payoffs to mating ( $M_1$  in Figure 1) and, thus, the more likely to desert for these reasons.

Hurtado and Hill (1988) tested hypotheses derived from mate desertion theory using data from two South American foraging societies, the Ache and Hiwi. Blurton Jones, Hawkes, Marlowe, and O’Connell (2000) extended the analyses to include two African foraging societies, the !Kung and Hadza. They argued that societies with higher pairbond stability should have: (a) higher payoffs for fathering effort, measured as differences between father-present and father-absent child mortality rates (i.e., the “fathering effect”); (b) lower payoffs for mating effort, as measured by fertility rates (i.e., fertility units per male, or FU/male); and, (c) a higher value for the tradeoff between the two, as measured by the parenting/mating index. As shown in Figure 3, they found that the payoff for mating was a better predictor of pairbond stability than the payoff for fathering. The tradeoff measure was also supported, albeit not as the predicted gradient. Blurton Jones et al. (2000) argued that their results cast doubt on previous accounts of the primacy of provisioning for the evolution of human pairbonding (Quinlan 2008).

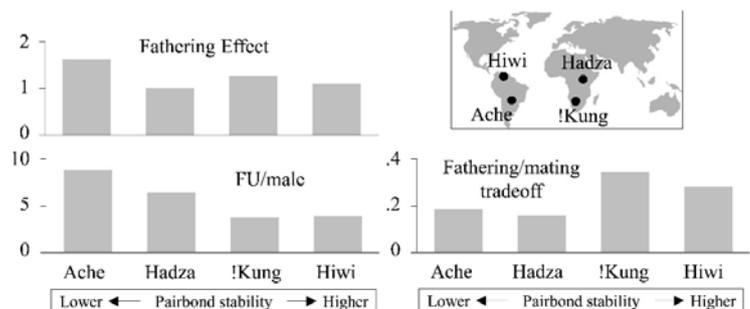
While paternal care may have an important function in supporting lactation (Marlowe, 2003; Quinlan & Quinlan, 2007, 2008), it does not covary as predictably with environmental uncertainty as does maternal care (Quinlan, 2007). In Sear and Mace’s (2008) review of studies of the effect of fathers on offspring survival, they found markedly mixed results with less than half showing a clear positive fathering effect. Studies of longer-term effects of fathers on offspring success appear mixed as well (e.g., Winking, Gurven, and Kaplan, 2011). This may be, in part, because children are cared for by a variety of kin and this may buffer children against father absence. Indeed, Quinlan

& Quinlan (2007) showed that availability of helpers led to higher incidence of divorce in a study of 58 small-scale societies. Taken together, the evidence supports Blurton Jones et al.’s (2000) contention that mating may trump fathering in the evolution of human pairbonding.

One of the most important aspects of the socioecological environment shaping the payoff to mating effort is the operational sex ratio (OSR)—a measure of the number of males to females currently available for mating. With a male-biased OSR, competition for mating opportunities is much more intense and, thus, males do better to stay in existing pairbonds; with a female-biased OSR, on the other hand, males may increase their fitness by deserting their mate (Blurton Jones et al., 2000; Ellsworth, Shenk, Bailey, & Walker, 2015). These hypotheses were overwhelmingly supported in a recent comparative study of pairbonding birds (Liker, Freckleton, & Székely, 2014), and there is accumulating evidence along the same lines in humans (e.g., Barber, 2003; Kruger, 2009).

### 2.3. Other Costs and Benefits in Ecological Context

The major shortcoming of mate desertion theory is that the actual benefits of pairbond stability go beyond the immediate parental care ramifications, and the actual costs



**Figure 3.** Fathering effect, FU/male, and their tradeoff in four societies ordered by pairbond stability, the inverse of divorce rates. Only the measure of payoff for mating effort, and less so the tradeoff measure, approximates the predicted gradient by pairbond stability. Created using data from Table 4.4 in Blurton Jones et al. (2000, p. 78).

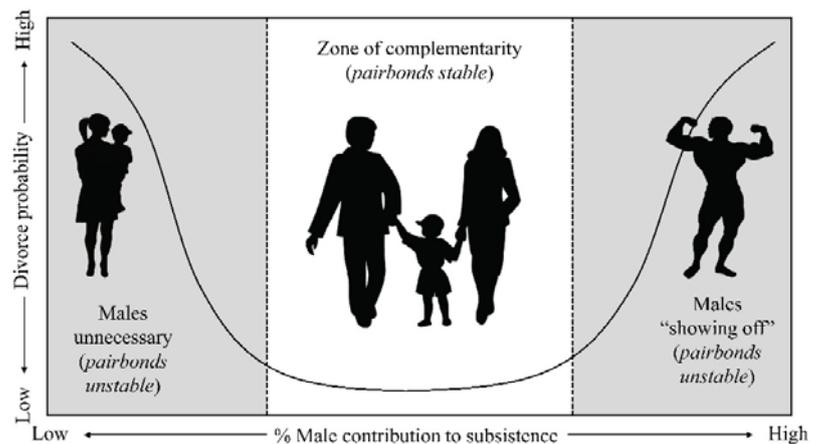
go beyond the current breeding attempt. Pairbond dissolution should be favored any time one or both in the pair can increase their fitness by seeking another mate. As Choudhury (1996) puts it, pairbond dissolution should be “viewed as a reproductive strategy by an individual to maximize its own fitness” and to ascertain an individual’s “net benefit from divorce one must compare the expected future gain in fitness with the new mate versus the expected gain with the old mate” (p. 414). Winking and Gurven (2011) measured these quantities with data from Tsimane hunter/horticulturalists from Bolivia, and concluded that males can increase their fitness via divorce.

Once one moves beyond mate desertion theory, however, little work has been done in developing quantitatively precise models of divorce that account for ecology. McNamara (1999), for example, built an ESS model of divorce, but it focused on intrinsic qualities of the partners rather than extrinsic qualities of the environment. The model predicted that high-quality individuals should be more likely to seek greener pastures than low-quality individuals, and that the most stable pairbonds will be between individuals of similar quality. This suggests that sexual conflict theory may be necessary to understand divorce, as the fitness increase enjoyed by the initiator is a fitness decrease for the abandoned. This appears to be true in at least some cases in humans. Käär, Jokela, Merilä, Helle, and Kojola (1998), for instance, showed that divorce led to increased reproductive success in males but not females in 18<sup>th</sup> to 20<sup>th</sup> Century Sami populations from Finland.

Marital satisfaction appears to hinge on ecologically variable factors that are closely tied to fitness (Shackelford & Buss, 1997; Dillon et al., 2015). Further, in a study of divorce using the Standard Cross-Cultural Sample—a database of 186 small-scale societies each coded for more than 2000 variables describing various aspects of typical behavior, beliefs, and environment—Betzig (1989) found that a handful of factors were associated with divorce, but most commonly infidelity and sterility. Both factors appear to cause divorce in industrialized societies as well (e.g., Barber, 2003), and both should also vary with socioecology. Economic opportunities were also associated with divorce in Betzig’s (1989) study, a result similar to those in industrialized societies (e.g., Barber, 2003). This mirrors trading-up-territories as a cause of pairbond dissolution in birds (Choudhury, 1996), which should occur in environments with marked variation in territory quality.

Economic considerations are central to Quinlan and Quinlan’s (2007) finding that subsistence complementarity was strongly related to pairbond stability in a multivariate study of data from the Standard Cross-Cultural Sample. In other words, divorce is a curvilinear function of percent male contribution to subsistence. As shown in Figure 4, when either males or females do the majority of subsistence work, there appears to be little reason to remain

pairbonded, though the reasons for this vary for the two non-complementary zones (Quinlan 2008). When females do the majority of the subsistence work, there may be no reason for males to stick around. When males do the majority of work, it may be that the work is geared toward “showing off” for potential future mates. Ellsworth et al. (2015) suggest their finding of a latitudinal gradient in marital stability but a lack of association with subsistence type may be due to latitudinal gradients in subsistence complementarity. Another possibility is that latitudinal gradients in pathogen distribution shape the fitness payoff for genetically diverse offspring, which could also lead to higher divorce rates (Low, 1990).



**Figure 4.** A schematic illustration of Quinlan & Quinlan’s (2007) discovery of, and explanation for, a strong association between pairbond stability and subsistence complementarity in the Standard Cross-Cultural Sample.

Resource predictability is another ecological factor that has been hypothesized to lead to pairbond instability. Weinrich (1977), for example, used evolutionary logic to ascribe contrasts in pairbonding strategies amongst US ethnic groups as a function of income predictability. Studies of pairbonding species might provide clues. For instance, Botero and Rubenstein (2012) found that environmental fluctuations and unpredictability were associated with divorce in a study of 163 bird species, suggesting that such flexibility in mating behaviour may serve to minimize the negative fitness consequences associated with ecological crossovers—i.e., where the fitness payoffs for one mating strategy are drastically reduced with sudden, drastic environmental changes. Other studies of humans, however, suggest that there is not such a simple link between the two. For instance, Cohen (2014) found that divorce rates *decreased* during the Great Recession of 2008-2011.

### 3. Conclusion

Human behavioral ecology brings evolutionary logic to bear on the problem of the ecology pairbond stability. Most work has centered on mate desertion theory, and its emphasis on the tradeoff between mating and parenting in males. This perspective is limited, however, as the costs and benefits of mate desertion go beyond the immediate effects on current offspring survival and the probability of finding a new mate. Models with a broader scope need to be developed, models incorporating a wider range of costs and benefits.

## References

- Barber, N. (2003). Divorce and reduced economic and emotional interdependence: A cross-national study. *J Div Remar*, 39, 113-124.
- Betzig, L. (1989). Causes of conjugal dissolution: a cross-cultural study. *Curr Anthropol*, 30(5), 654-676.
- Blurton Jones, N., Marlowe, F., Hawkes, K., & O'Connell, J. (2000). Paternal investment and hunter-gatherer divorce rates. *In* L. Cronk, N. Chagnon & W. Irons (Eds.), *Adaptation and human behavior: An anthropological perspective* (pp. 69-90). Hawthorne, NY: Aldine de Gruyter.
- Botero, C. A., & Rubenstein, D. R. (2012). Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. *PLoS ONE*, 7(2), e32311.
- Choudhury, S. (1995). Divorce in birds: a review of the hypotheses. *Anim Behav*, 50(2), 413-429.
- Cohen, P. N. (2014). Recession and divorce in the United States, 2008-2011. *Popul Res Policy Rev*, 33(5), 615-628.
- Dillon, L.M., Nowak, N., Weisfeld, G.E., Weisfeld, C.C., Shattuck, K.S., Imamoglu, O.E., Butovskaya, M., & Shen, J. (2015). Sources of marital conflict in five cultures. *Evol Psych*, 13(1), 1-15.
- Ellsworth, R., Shenk, M. K., Bailey, D. H., & Walker, R. S. (2015). Comparative study of reproductive skew and pairbond stability using genealogies from 80 small-scale human societies. *Am J Hum Biol*.
- Harpending, H., & Draper, P. (1986). Selection against human family organization. *In* B. J. Williams (Ed.), *On evolutionary anthropology: Essays in honour of Henry Hoijer* (pp. 37-75). Malibu, CA: Undena Press.
- Houston, A. I., Székely, T., & McNamara, J. M. (2013). The parental investment models of Maynard Smith: a retrospective and prospective view. *Anim Behav*, 86(4), 667-674.
- Hurtado, A. M., & Hill, K. (1992). Paternal effect on offspring survivorship among Ache and Hiwi hunter-gatherers: implications for modeling pair-bond stability. *In* B.S. Hewlett (Ed.), *Father-child relations: Cultural and biosocial contexts* (pp. 31-55). Hawthorne, NY: Aldine de Gruyter.
- Käär, P., Jokela, J., Merilä, J., Helle, T., & Kojola, I. (1998). Sexual conflict and remarriage in preindustrial human populations: causes and fitness consequences. *Evol Hum Behav*, 19(3), 139-151.
- Kruger, D. J. (2009). When men are scarce, good men are even harder to find: life history, the sex ratio, and the proportion of men married. *J Soc Evol Cult Psych*, 3(2), 93-104.
- Lazarus, J. (1990). The logic of mate desertion. *Anim Behav*, 39, 672-684.
- Liker, A., Freckleton, R. P., & Székely, T. (2014). Divorce and infidelity are associated with skewed adult sex ratios in birds. *Curr Biol*, 24, 880-4.
- Low, B. S. (1990). Marriage systems and pathogen stress in human societies. *Am Zool*, 30, 325-339.
- McNamara, J. M. (1999). An ESS model for divorce strategies in birds. *Phil Trans Roy Soc B*, 354(1380), 223-236.
- Marlowe, F. (2003). A critical period for provisioning by Hadza men: implications for pair bonding. *Evol Hum Behav*, 24, 217-229.
- Maynard Smith, J. (1977). Parental investment: a prospective analysis. *Anim Behav*, 25, 1-9.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. Princeton, NJ: Princeton U.P.
- Quinlan, R. J. (2007). Human parental effort and environmental risk. *Proc Roy Soc B*, 274(1606), 121-125.
- Quinlan, R. J. (2008). Human pair-bonds: evolutionary functions, ecological variation, and adaptive development. *Evol Anth*, 17, 227-38.
- Quinlan, R. J., & Quinlan, M. B. (2007). Evolutionary ecology of human pair-bonds: Cross-cultural tests of alternative hypotheses. *Cross-Cult Res*, 41(2), 149-169.
- Quinlan, R. J., & Quinlan, M. B. (2008). Human lactation, pair bonds, and alloparents: A cross-cultural analysis. *Hum Nat*, 19, 87-102.
- Sear, R., & Mace, R. (2008). Who keeps children alive: a review of the effects of kin on child survival. *Evol Hum Behav*, 29, 1-18.
- Shackelford, T., & Buss, D. M. (1997). Marital satisfaction in evolutionary psychological perspective. *In* R.J. Sternberg & M. Hojjat (Eds.), *Satisfaction in close relationships* (pp. 7-25). NY: Guilford Press.
- Weinrich, J. (1977). Human sociobiology: pair-bonding and resource predictability (effects of social class and race). *Beh Ecol Sociobiol*, 2(2), 91-118.
- Winking, J., & Gurven, M. (2011). The total cost of father desertion. *Am J Hum Biol*, 23(6), 755-763.
- Winking, J., Gurven, M., & Kaplan, H. (2011). Father death and adult success among the Tsimane: implications for marriage and divorce. *Evol Hum Beh*, 32, 79-89.
- Winterhalder, B., & Smith, E. A. (2000). Analyzing adaptive strategies: human behavioral ecology at 25. *Evol Anthropol*, 9, 51-72.