

1 Evolution, in press (accepted 3 January 2006)

2 **When not to avoid inbreeding**

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8

9 **Abstract**

10 Avoidance of incestuous matings is widely reported across many animal taxa, and the
11 adaptive value of such behaviour is explained through inbreeding depression. However, an
12 old and somewhat neglected theoretical result predicts that inbred matings offer another,
13 positive effect on the inclusive fitness of parents: an individual who mates with a relative will
14 help that relative to spread genes identical by descent. This benefit can be substantial, if the
15 additional mating achieved by the relative does not harm his mating success otherwise, and in
16 the context of selfing in plants the phenomenon is well known. Here, we develop a model that
17 derives expected values of inbreeding tolerance, i.e. the magnitude of inbreeding depression
18 that is required to make individuals avoid inbreeding, for different animal life histories and
19 parental investment patterns. We also distinguish between simultaneous and sequential mate
20 choice, and show that inbreeding tolerance should often be remarkably high in the latter
21 scenario in particular, although egalitarian parental care will lead to lower tolerance. There is
22 a mismatch between theory and data: the almost complete lack of cases where individuals
23 prefer to mate incestuously is at odds with a large overlap between the predicted range of
24 inbreeding tolerance and estimates of inbreeding depression found in nature. We discuss four
25 different solutions to this enigma, and suggest that inbreeding tolerance, where it is found,
26 should not always be attributed to a simple constraint that has prevented finding any other
27 mate.

28 **Introduction**

29 Inbreeding depression caused by mating with close relatives is a commonly reported
30 phenomenon in natural populations, although the exact magnitude of the reduction in fitness
31 caused by inbreeding is often not accurately known, and may depend on environmental
32 conditions (Keller & Waller 2002). It is consequently not surprising that inbreeding avoidance
33 is often reported and considered adaptive (Pusey & Wolf 1996; Amos et al. 2001), with
34 examples ranging from ants (Keller & Passera 1993) and field crickets (Simmons 1989, 1991;
35 Bretman et al. 2004) to primates (Pusey 1990). Often inbreeding avoidance leads to
36 considerable loss of breeding opportunities to the individual: e.g. in Siberian jays *Perisoreus*
37 *infaustus*, categorical inbreeding avoidance prevents territory inheritance that would
38 otherwise be adaptive for the offspring (Kokko & Ekman 2002), and females of naked mole-
39 rats (Cooney & Bennett 2000), meerkats (O’Riain et al. 2000) and acorn woodpeckers
40 (Koenig et al. 1999) likewise tend to remain reproductively inactive as long as no unrelated
41 males are available. In humans, the phenomenon is included as an item in the list of ‘human
42 universals’, i.e. characteristics of our species that seem to occur in every culture, as compiled
43 by Brown (1991).

44 ‘Too much’ outbreeding can have negative fitness consequences too, which is described by
45 the term outbreeding depression (Bateson 1978, 1982; Templeton 1986; Frankham 1995;
46 Pusey & Wolf 1996). Such cases arise if individual genomes host coadapted gene complexes,
47 making it maladaptive to break them down, or individuals are adapted to local conditions.
48 Outbreeding depression predicts ‘optimal outbreeding’ (Bateson 1983): only the closest kin
49 are avoided as mates to avoid close inbreeding, and the optimal mate is a (more or less)
50 distant relative, or a local mate as opposed to one from a distant population. To mention a
51 classic example, Bateson (1982) reports evidence that quail females have a preference for
52 cousins over either unrelated mates or brothers as mates.

53 Whether inbreeding avoidance or optimal outbreeding is considered, arguments are typically
54 based on maximizing the fitness of offspring. It has, however, been repeatedly pointed out
55 that mating with one’s own kin has an additional — and positive — effect on the parent’s
56 inclusive fitness (Bengtsson 1978, Parker 1979, Bateson 1983, Waser et al. 1986, Waller
57 1993, Lehmann & Perrin 2003). The argument presented below has, in the context of selfing,
58 been presented as early as 1941 by Fisher (1941). To develop the argument, let us first ignore
59 any negative fitness consequences of inbreeding, and consider a female that chooses to mate
60 with her brother instead of another, unrelated male. Also, let us assume that this mating does
61 not involve opportunity costs, or any other costs, to the male. In other words, the brother gains
62 an ‘additional’ mating with his sister without this affecting his success with other females.
63 Thus the female gains direct fitness (number of offspring n) through her offspring, but
64 additionally she gains indirect fitness rn by improving her brother’s mating success; total

65 inclusive fitness thus equals $(1+r)n$. Had she mated with an unrelated male, her inclusive
66 fitness would have remained as n , and mating with kin clearly in this case brought about a
67 substantial benefit.

68 Why don't then individuals of many species routinely prefer mating with kin? One possibility
69 is that any costs of inbreeding readily erode this benefit. Consider inbreeding depression of
70 magnitude δ , such that the fitness of inbred offspring is $1-\delta$ relative to 1 resulting from an
71 outbred mating. We have to compare the female's inclusive fitness from an inbred mating, $(1-$
72 $\delta)(1+r)n$, to outbred fitness n . In this case inbred matings are favoured if $\delta < r/(1+r)$. For full
73 sibs ($r = 0.5$) this means that brothers should be preferred over unrelated individuals as mating
74 partners due to the operation of kin selection, except if there is quite substantial inbreeding
75 depression that exceeds $\delta^* = 1/3$ (Parker 1979). Such high values are reported in the literature,
76 but by no means ubiquitously (Keller & Waller 2002). Parker (1979) also notes that a male
77 should strive to mate with his sister under even more general conditions: if the fitness loss is
78 anything less than $\delta^* = 2/3$.

79 In this paper our aim is to point out that the above calculation, despite having been reported in
80 the literature repeatedly (Parker 1979, Waser et al. 1986, Lehmann & Perrin 2003), presents a
81 serious mismatch between theory and data that has been very widely ignored. We construct a
82 model that shows that the value $\delta^* = 1/3$ for tolerating inbred matings is often (though not
83 always) an underestimate. When keeping track of the dynamics of the mating system,
84 including life history costs of breeding both for males and for females, preferences for
85 incestuous matings are often predicted under substantially stronger negative consequences of
86 inbreeding, although egalitarian parental care can also lead to the opposite prediction.
87 Egalitarian parental care does not suffice as a general explanation, however, as it is not the
88 norm in animal breeding systems. The almost complete absence of empirical studies reporting
89 kin preferences in animals thus remains enigmatic, and we discuss potential solutions to this
90 mystery.

91 **The model**

92 Our aim is to calculate the relative fitness consequences of incestuous matings by comparing
93 them with non-incestuous matings. Here, it is important to distinguish between two cases: one
94 where an alternative non-incestuous mating is immediately available (i.e. the individual is
95 finding itself in a simultaneous choice scenario), and one in which no other potential mate is
96 immediately available, but the choice is between mating with kin now or waiting for another
97 potential mate to appear. We call the latter the sequential choice scenario. In both
98 simultaneous and sequential choice situations, we first need to derive the fitness of individuals
99 who reject mating with kin, to see if preferences for kin can outcompete this strategy.

101 To achieve this, consider a population that follows the life cycle depicted in Figure 1. Both
 102 males and females begin their adult life by entering the mating pool, i.e. the ‘time in’ stage
 103 *sensu* Clutton-Brock & Parker (1992). We assume an even sex ratio at maturation. Individuals
 104 then spend the rest of their lives either being available as potential mates (‘time in’), or
 105 processing the consequences of the latest mating, in which case they are in a state called ‘time
 106 out’. Since they cannot breed again until they have completed this ‘time out’, the duration of
 107 this state for individuals of a given sex offers a convenient way to model parental investment.
 108 Such investment includes parental care, but also any form of mating investment that is ‘used
 109 up’ in a single mating, e.g. large spermatophores — whereas the possession of a sexual
 110 ornament that is not used up in a mating is not included. Hence, regardless of his secondary
 111 sexual traits, ‘time out’ will be short for a non-caring male mammal if he can replenish sperm
 112 supplies quickly, but for a female of the same species ‘time out’ is not over before the
 113 offspring are weaned. The length of time out will accordingly have a strong influence on
 114 potential reproductive rates, the operational sex ratio, and sex-specific mate encounter rates
 115 (Clutton-Brock & Parker 1992; Kokko & Monaghan 2001). We assume mortality operates at
 116 a constant rate for an individual in a given state (e.g., for a female in ‘time in’), and mate
 117 encounter rates are similarly constant over time; in other words, we assume a continuous-time
 118 setting with no age structure.

119 To maintain generality, we label sexes as the ‘choosing sex’ and the ‘opposite sex’, which
 120 allows interpreting our results in the context of either female or male mate choice. We will
 121 use the reproductive value approach to calculate fitness, described in detail in e.g. Härdling et al.
 122 al. (2003); van Boven & Weissing (2004); Schmelzer et al. (2005). The reproductive values
 123 will depend on an individual’s state: an individual in a ‘time in’ state will have a different
 124 expected long-term contribution to future generations than one in ‘time out’, and the
 125 difference in reproductive values will reflect this expectation (Houston & McNamara 1999).
 126 This allows us to calculate the consequences of a specific decision, such as accepting or
 127 refusing a potential mate. Refusal means staying in ‘time in’, while acceptance leads to
 128 offspring production but also changes the parent's reproductive value as it must now enter the
 129 ‘time out’ state. The individual should breed if the sum of the value of offspring produced
 130 plus the change in the parent’s own reproductive value is positive (Houston & McNamara
 131 1999).

132 We denote the ‘time in’ reproductive value of individuals of the choosing sex by v_I , and that
 133 of opposite-sex individuals by w_I . The reproductive values during ‘time out’ will be v_O and w_O
 134 for the choosing and the opposite sex, respectively. Individuals in ‘time in’ encounter
 135 unrelated potential mates at a rate M if the operational sex ratio is unbiased. The resulting
 136 mating rate is $m_v = M\sqrt{\beta}$ for the choosy sex and $m_w = M/\sqrt{\beta}$ for the opposite sex, when
 137 the operational sex ratio (males : females) equals β (see Kokko & Monaghan 2001). Mating

138 leads to offspring production, yielding a direct fitness benefit $a(w_1+v_1)$. This corresponds to
 139 $2a$ mature offspring of each sex, each related to the parent by $1/2$. We constrained our study to
 140 values of a that ensure population stability (see Appendix). After mating, both parents enter
 141 the 'time out' state, and its duration can be very different for the two sexes (Figure 1).

142 Denoting the mean duration as T_v for the choosing sex and T_w for the opposite sex, we will
 143 often have $T_v > T_w$ as individuals of the choosing sex typically invest more in offspring
 144 (Clutton-Brock & Parker 1992). This imbalance will also be reflected in the operational sex
 145 ratio, β (see Appendix). Making the time out explicitly modelled takes into account the
 146 number of outbred matings forfeited as a result of accepting an inbred mating, which has been
 147 shown to be crucial to the question (Waser et al. 1986).

148 Individuals can also die at any stage of their life, and the mortalities are μ_{Iv} , μ_{Ov} , μ_{Ow} and μ_{Iw}
 149 as indicated in Figure 1. The mating system leads to an interdependency of the reproductive
 150 values v_I , v_O , w_O and w_I , which are calculated as indicated in the Appendix. These are the
 151 baseline fitness values that we need for comparing the mate choice strategies in the following
 152 section.

153 SIMULTANEOUS MATE CHOICE

154 Now consider a case where a choosy individual has encountered two potential mates and can
 155 choose between them. One of them is unrelated to the focal individual, and the other one is
 156 related with relatedness coefficient r (for full sibs, $r = 0.5$). Inbreeding depression is
 157 expressed as δ : if the female mates incestuously, a fraction δ of her offspring die that
 158 otherwise would have survived (as in e.g. Parker 1979; Lehmann & Perrin 2003).

159 If the focal individual mates non-incestuously in this case, it enters the 'time out' stage with
 160 reproductive value v_O , while the related potential mate (who did not mate) remains at w_I . The
 161 reproductive gain is worth $a(v_I+w_I)$. If the focal individual mates incestuously, its own
 162 reproductive value becomes v_O as above, the related mate's value changes to w_O , and both
 163 parents gain a direct benefit $(1-\delta)a(v_I+w_I)$. Given relatedness r , the inclusive fitness
 164 consequences for the focal choosy individual are

165 mate with non-kin: $v_O + r w_I + a(v_I + w_I)$

166 mate with kin: $v_O + r w_O + (1+r)(1-\delta)a(v_I + w_I)$

167 These expressions avoid the double-accounting problem (Creel 1990), and the latter quantity
 168 is larger — and kin matings thus preferred — if δ is smaller than the threshold value for
 169 simultaneous choice,

$$170 \quad \delta^*_{\text{sim}} = \frac{ar(v_I + w_I) - r(w_I - w_O)}{a(1+r)(v_I + w_I)}. \quad (1)$$

171 We call this quantity the inbreeding tolerance in simultaneous choice scenarios. Note that
 172 this reduces to the ‘classical’ criterion $\delta < r/(1+r)$ (Parker 1979; Lehmann & Perrin 2003) if
 173 opposite-sex reproductive values w_0 and w_1 do not differ from each other, which implies that
 174 the choosy sex is the sole provider of parental care, and there are no other costs of mating to
 175 the opposite sex. These are indeed the conditions outlined in Parker (1979).

176 SEQUENTIAL CHOICE

177 Now consider the case where the choosy individual has encountered only one potential mate,
 178 and relatedness equals r . The fitness consequences of mating with kin are as in the
 179 simultaneous choice scenario. The difference is that instead of being able to choose between
 180 related and unrelated individuals, the individual has to make a choice between mating with the
 181 related individual and refusing to mate for the time being. The latter option implies that both
 182 individuals stay in the ‘time in’ state until another potential mate appears for either of them.
 183 Fitness consequences of mating therefore now have to be compared against a scenario where
 184 both ‘self’ and ‘kin’ simply stay in the ‘time in’ state. This option gives an inclusive fitness
 185 value of $v_1 + r w_1$. Including v_1 and w_1 in the comparison takes into account that the costs of
 186 not mating will depend on the prospects of finding another mate soon, and these prospects in
 187 turn depend on the numbers of same- and opposite-sex individuals searching for mates (and
 188 thus ultimately on parameters such as the duration of the ‘time out’; see Appendix for the
 189 calculation of v_1 and w_1). It follows that mating is now favoured if the inbreeding depression δ
 190 falls below the threshold

$$191 \quad \delta_{\text{seq}}^* = \frac{a(1+r)(v_1 + w_1) - (v_1 - v_0) - r(w_1 - w_0)}{a(1+r)(v_1 + w_1)} = 1 - \frac{(v_1 - v_0) + r(w_1 - w_0)}{a(1+r)(v_1 + w_1)} \quad (2)$$

192 This quantity is the inbreeding tolerance of individuals in sequential choice scenarios. High
 193 costs of breeding (high ‘time in’ reproductive values compared to ‘time out’ values) decrease
 194 the tolerance, while a low value of the current breeding attempt (low a ; note that offspring of
 195 one breeding attempt are worth $a(v_1 + w_1)$) increases the tolerance and thus makes a preference
 196 for incestuous matings more likely. Note that low a arises automatically (Appendix) if there
 197 are many breeding attempts in an individual’s lifetime.

198 Results

199 Inbreeding tolerance is highly context-dependent: Simultaneous and sequential mate choice
 200 scenarios can show very different values (figures 2-3). When an individual has to perform
 201 sequential choice, inbreeding avoidance means that both it and its mate lose all current
 202 reproductive benefits by not breeding immediately. In particular if mate encounter rates are
 203 low for at least one of the sexes (figure 3), this implies that inbreeding should be much more
 204 tolerated when mates are encountered sequentially, than when the individual can compare two

205 or more mates simultaneously. Under conditions of very high mate availability, the
 206 difference between simultaneous and sequential choice vanishes (figure 3).

207 Parker (1979) concluded that when sex roles are well differentiated such that one sex provides
 208 all the parental care, the choosy sex should have inbreeding tolerance $1/3$ in full sib matings (r
 209 $= 0.5$), whereas the opposite sex should ‘want’ to mate with inbreeding depression reaching as
 210 high values as $2/3$. Figure 2 supports this and shows how intermediate scenarios with less
 211 extreme sex roles link these two cases. Perhaps surprisingly, intermediate cases in terms of
 212 sex roles are not necessarily intermediate regarding their inbreeding tolerance. In Figure 2a,
 213 the choosing sex has a considerable time out $T_v = 0.1$ (compared to the expected lifespan
 214 which equals 1 in all our examples). Towards the left of the figure, the opposite sex has a
 215 much shorter time out and can thus be considered a non-caring male; here, the choosy sex
 216 prefers to mate incestuously with tolerance $\delta^* = 0.33 \approx 1/3$. Towards the right end of the
 217 figure, the opposite sex has a very high time out $T_w = 100$. A very high time out can be
 218 interpreted as semelparity: there is virtually no chance that an individual can live to a second
 219 breeding attempt. The sex with the lower time out (enabling several breeding attempts for one
 220 of the sexes), $T_v = 0.1$, can now be interpreted as being the male. His parental investment is
 221 certainly lower than that of the semelparous female, but perhaps sufficiently high to make him
 222 choosy (Kokko & Monaghan 2001). The tolerance has now climbed to $\delta^* = 0.66 \approx 2/3$. In
 223 between, however, tolerance values do not climb smoothly from $1/3$ towards $2/3$, but
 224 experience a considerable dip where parental investment is roughly equal, $T_v = T_w = 0.1$. At
 225 this point of egalitarian parental care, both parents should avoid inbreeding when the fitness
 226 costs to offspring exceed 10% (Figure 2a).

227 Figure 2b describes a similar setting, but now the choosy sex breeds quickly and very
 228 iteroparously, $T_v = 0.01$. As noted in the context of deriving equation (2), this results in a
 229 relatively low value of each breeding attempt. Fitness is more strongly determined by how
 230 many times the individual can complete a breeding cycle; loosely speaking, each breeding
 231 cycle is ‘taken less seriously’ by the breeders, and individuals accept any mate almost
 232 regardless of how valuable the offspring are, as long as inbreeding depression does not make
 233 them almost completely unviable. In other words, inbreeding tolerance increases in this case,
 234 and choosy individuals — even if they are females who are the sole providers of the parental
 235 care (left side of figure 2b) — show inbreeding tolerance values much higher than $1/3$. Again,
 236 the lowest tolerance of inbreeding occurs when the two sexes invest roughly (but not exactly)
 237 equally in parenting (figure 2b), although the dip is in this case not deep.

238 Under simultaneous choice, the results are far simpler. Full-sib relatedness $r = 0.5$ leads to
 239 values close to the classical threshold $r/(1+r) = 1/3$ when the choosy sex has the higher time
 240 out. When the choosy sex is the one that invests less, the threshold drops to close to zero. The
 241 results are easy to explain. Consider a species with conventional sex roles, females providing

242 all the parental care, and male reproductive success being limited by their access to females.
 243 The first scenario (left sides of figures 2a-b, e.g. $T_w < 0.001$) corresponds to a female who has
 244 encountered two males, a relative and an unrelated male. She should take into account that the
 245 related male does probably not have access to any other females at the moment, and he can
 246 gain an additional, cost-free mating (i.e. no opportunity or parental care costs) if she mates
 247 with him. Thus, the equations of Parker (1979) apply. The second scenario is described by
 248 high values of the opposite-sex time out T_w (e.g. $T_w > 0.1$ in figures 2a-b). Since $T_w > T_v$, the
 249 interpretation for a conventional species is that a *male* has been lucky enough to locate two
 250 receptive females simultaneously: a sister and an unrelated female. Now, the sister is unlikely
 251 to have any trouble locating additional mates, thus there is no indirect benefit gained by
 252 allowing her to mate right now, and only a cost of producing inferior offspring. Therefore,
 253 now the slightest negative consequences of inbreeding should make the male prefer mating
 254 with the unrelated female (assuming that she is receptive and willing to accept the current
 255 male — as is assumed under our simultaneous choice scenario).

256 Figure 3 additionally explores the effects of the species-specific mate encounter rate, M , from
 257 which the sex-specific encounter rates are derived. Low values of M mean that the
 258 reproductive success is badly limited by mate availability in at least one of the sexes. The
 259 potential to gain indirect benefits by allowing the opposite sex to mate increase under such
 260 conditions. Additionally, the choosy individual's own prospects of finding additional mates
 261 are poor when M is low, thus it cannot be too fastidious regarding the current mating
 262 opportunity. These two processes together mean that when mate availability is severely
 263 limited, inbreeding tolerance under sequential choice can reach values that even exceed 2/3
 264 (figure 3).

265 As before, egalitarian parental care with high mate availability bring about the best conditions
 266 for strict inbreeding avoidance (right end of figure 3b). However, these factors do not help to
 267 diminish the tolerance below 1/3 in strongly iteroparous species (figure 3c). Instead, in this
 268 case the tolerance can remain substantially higher than 1/3 even if mates are encountered
 269 quite frequently: sequential choice in figure 3c, where breeding is quick ($T_v = T_w = 0.01$)
 270 predicts that individuals should accept incestuous matings leading to fitness loss of more than
 271 50%, even if mate availability is moderately high ($M = 100$; figure 3c).

272 **Discussion**

273 Our results expand on earlier ones (Parker 1979; Lehmann & Perrin 2003) that show that
 274 there is a substantial kin-selected benefit to mating incestuously. Our model not only shows
 275 that the equation for preferential sib mating — $\delta < 1/(1+r)$ — should be taken seriously, but
 276 also that it often underestimates the magnitude of inbreeding depression that individuals
 277 should tolerate. The inbreeding tolerance δ^* is often larger than 1/3 for full-sib matings,
 278 particularly if mate choice is sequential rather than simultaneous. The tolerance can even

279 exceed 2/3, the result previously described for males whose reproductive success is solely
280 determined by the number of mating partners (Parker 1979). Yet the empirical literature is
281 almost exclusively focused on inbreeding avoidance.

282 Our results predict that species that are capable of breeding many times in their lifetime, but
283 whose reproductive success is limited by low mate encounter rates, should show the highest
284 inbreeding tolerance. However, extreme life histories are not required for moderately high
285 tolerance, e.g., 1/3 for sib matings. Observed levels of inbreeding depression in wild
286 populations vary widely (Keller & Waller 2002). While our model by no means precludes the
287 evolution of inbreeding avoidance or states it should be infrequent, the wide variation both in
288 the predicted inbreeding tolerance and in inbreeding depression found in nature certainly
289 predicts that preferences for inbred matings (over non-inbred ones, or over waiting for another
290 potential mate) should at least *sometimes* be seen. This means that it remains a mystery why
291 preferences for incestuous matings are hardly ever reported in animals. Meanwhile, in the
292 botanical literature selfing is often explained adaptively. A selfing gene transmits itself 50%
293 more efficiently to offspring. This factor, equivalent to our kin-selected benefit, is routinely
294 included in calculations of the fitness of selfing individuals (e.g., Lloyd 1979; Charlesworth
295 1980; Uyenoyama et al. 1993; Rauscher & Chang 1999; Cheptou & Mathias 2001).

296 We now discuss four possible reasons behind this apparent mismatch between theory and
297 data.

298 SOLUTION 1. CONDITIONS THAT PREDICT LOW INBREEDING TOLERANCE ARE THE NORM

299 Our model predicts that inbreeding tolerance can sometimes deviate downwards from the
300 classical values 1/3 (females) and 2/3 (males). The mismatch between theory and data is
301 consequently solved if breeding systems that produce low tolerance can be shown to be
302 common. However, the conditions required are that both sexes invest roughly equally — and
303 fairly substantially — in offspring, and the mate encounter rate is high. Neither sex then has
304 much difficulty locating additional mates, thus it is not very costly to either individual that a
305 current incestuous mating opportunity is rejected by one of the mates, whereas taking
306 advantage of the mating opportunity implies substantial parental effort from both sides for a
307 small reward in the form of inbred offspring. The field of sexual selection abounds with
308 examples where parental care is not egalitarian, however, and reproductive success in at least
309 one of the sexes (typically males) is limited by access to mates (Andersson 1994). Thus our
310 first solution fails as a general explanation for an ubiquitous lack of kin preferences in the
311 context of mating.

312 A perhaps more likely version of this explanation is that mate choice much more often
313 resembles our simultaneous scenario, which systematically leads to lower tolerance values,
314 than the sequential scenario. If mate choice is a seasonally occurring quick and intense event,

315 it is possible that choosy individuals can during this time compare different potential mates
316 simultaneously or at least in very rapid succession. The predictions of the simultaneous and
317 the sequential scenario indeed become identical when the mate encounter rate M is very high
318 (figure 3). Nevertheless, under this scenario the predicted tolerance often saturates near $1/3$,
319 rather than zero, and it is therefore an unlikely explanation for a near complete absence of
320 preferences for incestuous matings in the literature.

321 SOLUTION 2. MODELS FAIL TO CAPTURE REALITY PROPERLY

322 Models are always approximations, and it is possible that ours fails to capture something
323 crucial about the nature of inbreeding. Above, we already discussed seasonal mating seasons,
324 which were not explicitly modelled here. Other factors not explicitly included are the details
325 of the genetic architecture and the purging process, whereby deleterious alleles are selected
326 against and disappear from the gene pool when inbreeding occurs over several generations
327 (Wang et al. 1999; Crnokrak & Barrett 2002; Glémin 2003). This can alter the course of
328 evolution of the mating system (Waller 1993; Peer & Taborsky 2005). Explicit modelling is
329 required to resolve how this would change our conclusions, but at least at first sight purging
330 appears unlikely to reduce our inbreeding tolerance levels: rather, purging should eventually
331 make inbreeding depression less severe, and thus allow individuals to pay more, rather than
332 less, attention to the kin-selected benefits of inbreeding. In the context of the evolution of
333 selfing, the effect of purging has been found to be minor (Charlesworth et al. 1990).

334 Another important simplification is that we assume that the invasion prospects of an
335 inbreeding mutant can be calculated using Hamilton's rule (with benefits and costs self-
336 consistently derived using the currency of reproductive value, see McNamara & Houston
337 1986). This is an approximation that may not hold true when explicitly tracking the fate of
338 dominant (or recessive) alleles that cause sib matings. An explicit population genetic
339 approach studying this question could be fruitfully combined with an examination with the
340 purging process and other aspects of inbreeding that can change with the evolving genetic
341 structure of an inbreeding population. In the meanwhile, it is reassuring that phenotypic
342 invasion approaches and explicit genetic models have yielded convergent results in the study
343 of selfing in plants (e.g., Lloyd 1992; Rausher & Chang 1999; Morgan et al. 2005).

344 A further theoretical avenue worth exploring is the interaction between mate quality and
345 relatedness. It is not immediately obvious in which direction this will change the inbreeding
346 tolerance. Females should be particularly prone to aid their brothers to reproduce if these are
347 of low quality and therefore have otherwise low mating success, but in this case the female
348 also has to pay the extra cost of foregoing the chance to have high quality males as sires of her
349 offspring. It should also be noted that inbreeding itself may directly affect the phenotypic
350 expression of mating behaviour (Chapman et al. 2003; Martin & Hosken 2004).

351 SOLUTION 3. INBREEDING DEPRESSION UNDERESTIMATED IN NATURE

352 Inbreeding depression is difficult to estimate in nature. Often it is only expressed under
353 particularly harsh conditions, and examining benign conditions only may reveal little about
354 the relationship between fitness and the genetic composition of individuals (Keller et al. 1994;
355 Pusey & Wolf 1996; Lens et al. 2000; Keller & Waller 2002; Joron & Brakefield 2003).
356 Under temporally varying selection, an evolutionary strategy cannot be successful if it only
357 performs well in benign environments, even if harsh conditions occur infrequently (e.g. Léon
358 1985; McNamara 1995; Benton & Grant 1996). Thus, inbreeding avoidance could be adaptive
359 because outbred offspring perform well during particularly harsh conditions that the
360 population experiences once in a while — even if a calculation of inclusive fitness during a
361 ‘normal’ year would indicate that the inbreeding depression falls below the tolerance
362 threshold δ^* .

363 An additional difficulty is that it is not always easy to estimate how benign or harsh
364 environmental conditions are, either in the laboratory or in the wild (e.g. Cheptou & Mathias
365 2001; Henry et al. 2003; Joron & Brakefield 2003). Females may also differ in their mating
366 behaviour depending on their own mating history (e.g., Johnstone & Keller 2000; Kokko &
367 Mappes 2005), and effects of inbreeding may be differentially expressed in male and female
368 offspring (Saccheri et al. 2005). Small inbreeding effects in many fitness components could
369 add up to significant effects on total fitness. In particular, the mating success of male
370 offspring can be a particularly sensitive trait regarding inbreeding depression (Joron &
371 Brakefield 2003; Ahtiainen et al. 2004; Reid et al. 2005), but studies often neglect measuring
372 it. To make matters still worse for the empiricist, inbreeding coefficients themselves are hard
373 to measure in the wild: molecular metrics are often only weakly correlated with inbreeding
374 coefficients (Pemberton 2004). Using heterozygosity as a proxy for inbreeding coefficients
375 can therefore easily lead to flawed results.

376 SOLUTION 4. EMPIRICAL EVIDENCE EXISTS IF WE LOOK FOR IT

377 Finally, we consider it a real possibility that the perception of ubiquitous inbreeding
378 avoidance in nature follows from a mistaken view that it is the theoretical expectation. It
379 certainly appears to be the case that behavioural ecologists are unaware of Parker’s (1979)
380 prediction, or the conceptual similarity between results on selfing and biparental inbreeding
381 (Waller 1993). To mention just one example, Cohen and Dearborn (2004) have recently
382 reported highly intriguing data on great frigatebirds *Fregata minor*. These birds seem to
383 actively choose genetically similar individuals as mates, and the authors provide a balanced
384 discussion of several alternative adaptive explanations behind this pattern. Yet, kin selection
385 is not mentioned among the alternatives.

386 The frigatebird study is not an isolated example: a review on inbreeding avoidance in
387 animals (Pusey & Wolf 1996) fails to mention the theoretical prediction that inbreeding
388 depression has to exceed a substantial threshold value before any avoidance behaviour is
389 expected to evolve. Consequently, when incestuous mating is observed, researchers tend to
390 ‘explain it away’ as a result of a constraint. To name one example, a study of incest avoidance
391 in shorebirds (Blomqvist et al. 2002) showed that females paired to genetically similar mates
392 had more extra-pair paternity in their nests. But why was inbreeding a problem in the first
393 place in a large population consisting of highly mobile individuals? A more challenging
394 interpretation is to ask why there was at least a preference for incestuous matings over not
395 breeding (many cooperative breeders opt for the latter, Koenig et al. 1999; Cooney & Bennett
396 2000; O’Riain et al. 2000; Kokko & Ekman 2002) or accepting dispersal costs to breed
397 elsewhere (Pärt 1996; Perrin & Mazalov 2000).

398 Such a change in the point of view would help to focus on the conditions under which
399 inbreeding avoidance is unnecessary or even harmful. There are several well-known taxa such
400 as social spiders (Riechert & Roeloffs 1993), bark beetles (Jordal et al. 2002) and termites
401 (Goodisman & Crozier 2002) in which inbreeding can be the rule rather than the exception,
402 but lack of avoidance has also been reported e.g. in field crickets (Jennions et al. 2004), coal
403 tits (Schmoll et al. 2005) and dwarf mongoose (Keane et al. 1996). Some studies report
404 surprisingly strong inbreeding in species that ought to be able to avoid incestuous matings due
405 to large population size and high mobility (e.g. plaice *Pleuronectes platessa*, Hoarau et al.
406 2005, and tree swallow *Tachycineta bicolor*, Shutler et al. 2004). Other cases that should be
407 studied further as they hint at active kin preferences include Colorado potato beetles
408 *Leptinotarsa decemlineata* in which siblings achieve copulation more often than non-siblings
409 in controlled laboratory conditions (Ots et al. submitted), barn swallows that show higher
410 relatedness between extra-pair than within-pair mates (Kleven et al. 2005), and flour beetles
411 *Tribolium castaneum* in which mating probabilities increase when the female and the male
412 share the same genotype (Nilsson et al. 2002). Several studies additionally report lack of
413 inbreeding avoidance together with non-significant tendencies to prefer kin matings (e.g.,
414 Glanville fritillary butterfly *Melitaea cinxia*, Haikola et al. 2004; great reed warbler
415 *Acrocephalus arundinaceus* in extra-pair contexts, Hansson et al. 2004). The prediction of
416 higher inbreeding tolerance in males than females has been elegantly confirmed in a study of
417 sperm use in feral fowl (Pizzari et al. 2004).

418 CONCLUSIONS

419 We do not predict that the numerous studies reporting inbreeding avoidance (Pusey & Wolf
420 1996) are all wrong. Nevertheless, the conditions under which one should expect inbreeding
421 avoidance are stricter than is often assumed. On the other hand, measuring inbreeding
422 depression is not easy, and the real cost of inbreeding may often have been underestimated.

423 There is currently mixed evidence e.g. for the role of relatedness in determining extra-pair
424 copulation patterns in birds (Blomqvist et al. 2002; Foerster et al. 2003; Hansson et al. 2004;
425 Kleven et al. 2005; Schmoll et al. 2005). Given the overlap between reported inbreeding
426 depression values in the literature and the large range of inbreeding tolerance values predicted
427 by our model, such a mixed pattern is perhaps the expected one. From an overlap it also
428 follows that the costs and benefits of inbreeding will often roughly balance. Selection pressure
429 to prefer or to avoid kin can therefore become weak, including selection to evolve efficient
430 kin recognition mechanisms. Therefore, lack of inbreeding avoidance that results from an
431 inability to recognize kin does not necessarily mean that the organism is trapped in
432 suboptimal behaviour due to a cognitive constraint. Alternatively, a failure to evolve kin
433 recognition can also follow if animals simply do not typically encounter kin in a mating
434 context.

435 Our model predicts that mating decisions should often differ between simultaneous and
436 sequential scenarios. A general practice in mate choice studies is to conduct simultaneous
437 choice experiments. It is, of course, natural to give animals the choice when studying choosy
438 behaviour, but the value of alternative approaches is increasingly recognized (Peretti &
439 Carrera 2005; Schäfer & Uhl 2005; Shackleton et al. 2005). The question of a proper
440 experimental setup is extremely important in the current context: sequential choice, where
441 alternative mates are not readily available, can predict substantial increases in inbreeding
442 tolerance (Bilde et al. 2005), symptomatic of a general reduction in choosiness (Kokko &
443 Mappes 2005).

444 The most intriguing experimental prospects arise if animals often cannot make a simultaneous
445 choice between two or more potential mates, but now and then such an opportunity arises. If
446 both cases have occurred often enough in evolutionary history, individuals are expected to
447 possess reaction norms (plastic preferences) that produce the appropriate response to each
448 situation. In many cases, our model then predicts switching between preference and avoidance
449 of kin as mates. Therefore, a male fish in a chambered aquarium who sees two females, both
450 ready to spawn with him, should ignore his sister and court the other female, yet in a more
451 natural setting with limited mating opportunities he might well do better preferring to mate
452 with her (and she should often prefer him over unrelated males, if he had trouble reproducing
453 otherwise). We therefore encourage more research linking the consequences of inbreeding in
454 natural populations with behavioural studies of mate preferences both in males and in
455 females.

456 **Acknowledgements.** We thank Jari Ahtiainen, Rob Brooks, Kevin Foster, Michael Jennions, Jonathan Jeschke,
457 Jan Lifjeld, Jan Lindström, Andrés López-Sepulcre, Geoff Parker and Tom Tregenza for comments and inspiring
458 discussions, and two anonymous referees for very helpful and constructive suggestions. Funding was provided
459 by the Academy of Finland (to HK) and by the Estonian Science Foundation (grants # 4586 and 6473, to IO).

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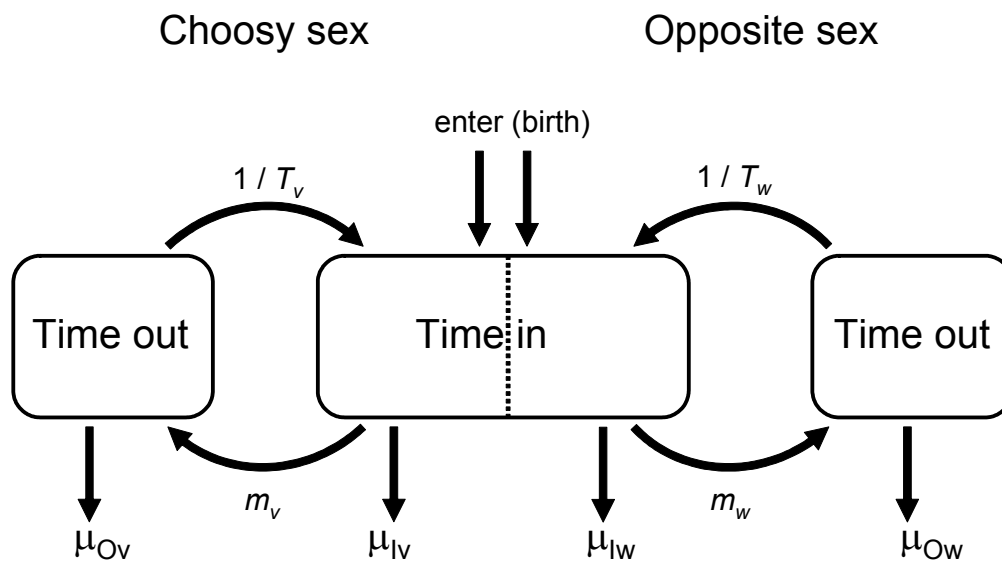
621 **Appendix**

622 Figure (1) leads to reproductive values as given by the matrix

$$623 \begin{pmatrix} dv_1/dt \\ dv_0/dt \\ dw_1/dt \\ dw_0/dt \end{pmatrix} = \underbrace{\begin{pmatrix} -\mu_{1v} + m_v(a-1) & m_v & am_v & 0 \\ 1/T_v & -1/T_v - \mu_{0v} & 0 & 0 \\ am_w & 0 & -\mu_{1w} + m_w(a-1) & m_w \\ 0 & 0 & 1/T_w & -1/T_w - \mu_{0w} \end{pmatrix}}_{\mathbf{A}} \begin{pmatrix} v_1 \\ v_0 \\ w_1 \\ w_0 \end{pmatrix} \quad (\text{A.1})$$

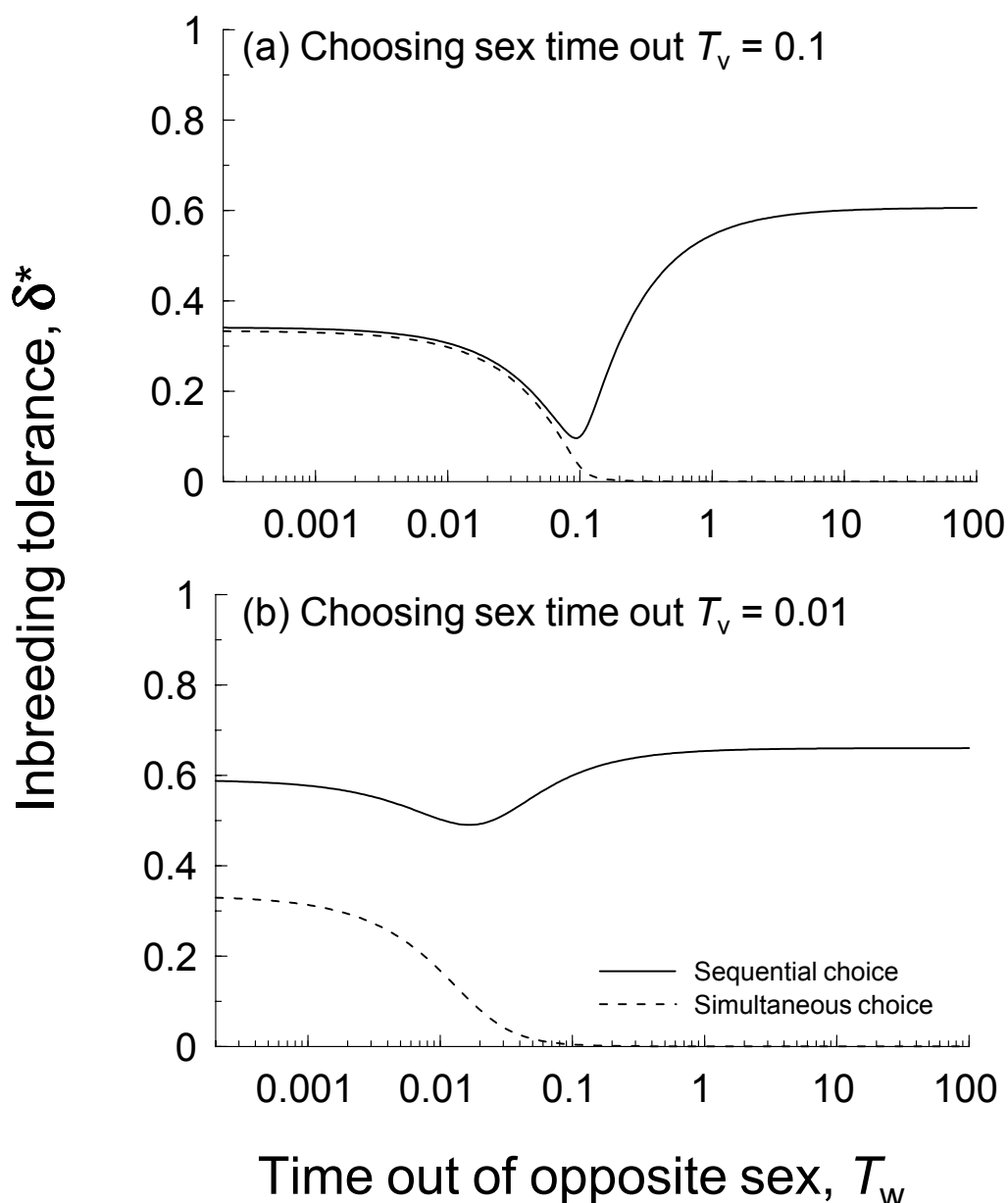
624 Here e.g. the first row results from noting that dv_1/dt , the change in reproductive value for a
 625 female in the ‘time in’ state, depends on the mating rate m_v , and on the death rate μ_{1v} . Mating
 626 leads to direct fitness increase $a(v_1 + w_1)$, but also to the replacement of the individual’s own
 627 ‘time in’ reproductive value v_1 by the ‘time out’ value v_0 . The net change due to mating is
 628 therefore $m_v [(a-1)v_1 + v_0 + aw_1]$, and due to death, $-\mu_{1v}v_1$ (for a mathematical justification of
 629 this method, see Härdling et al. 2003). These are expressed in matrix format in equation (A.1).
 630 The values of m_v depend on the operational sex ratio β as $m_v = M\sqrt{\beta}$ (see main text). β is
 631 calculated according to equation (3) in Kokko & Monaghan (2001), where the model
 632 population follows an equivalent life cycle. The value a is chosen such that each mature
 633 individual of the choosy sex produces, on average, one mature offspring of the same sex,
 634 which implies a stable population regulated by the probability that a newly born offspring
 635 recruits into the population as a mature adult. From (A.1) it follows that a newly matured
 636 individual of the choosy sex reproduces, on average, $m_v(1/T_v + \mu_{1v}) / (\mu_{0v}/T_v + \mu_{1v}(m_v + \mu_{0v}))$
 637 times before death, thus a is given by the equation $2a = [m_v(1/T_v + \mu_{1v}) / (\mu_{0v}/T_v +$
 638 $\mu_{1v}(m_v + \mu_{0v}))]^{-1}$.

639 This value of a leads to an eigenvalue $\lambda = 1$ of the matrix $(\mathbf{A} + \mathbf{I})$, where \mathbf{I} is the 4×4 identity
 640 matrix (for a justification see e.g. Härdling et al. 2003). The associated eigenvalue gives the
 641 relationship between the values v_1 , v_0 , w_1 and w_0 . In practice, these eigenvalues are calculated
 642 numerically, as the analytical solution is unwieldy.



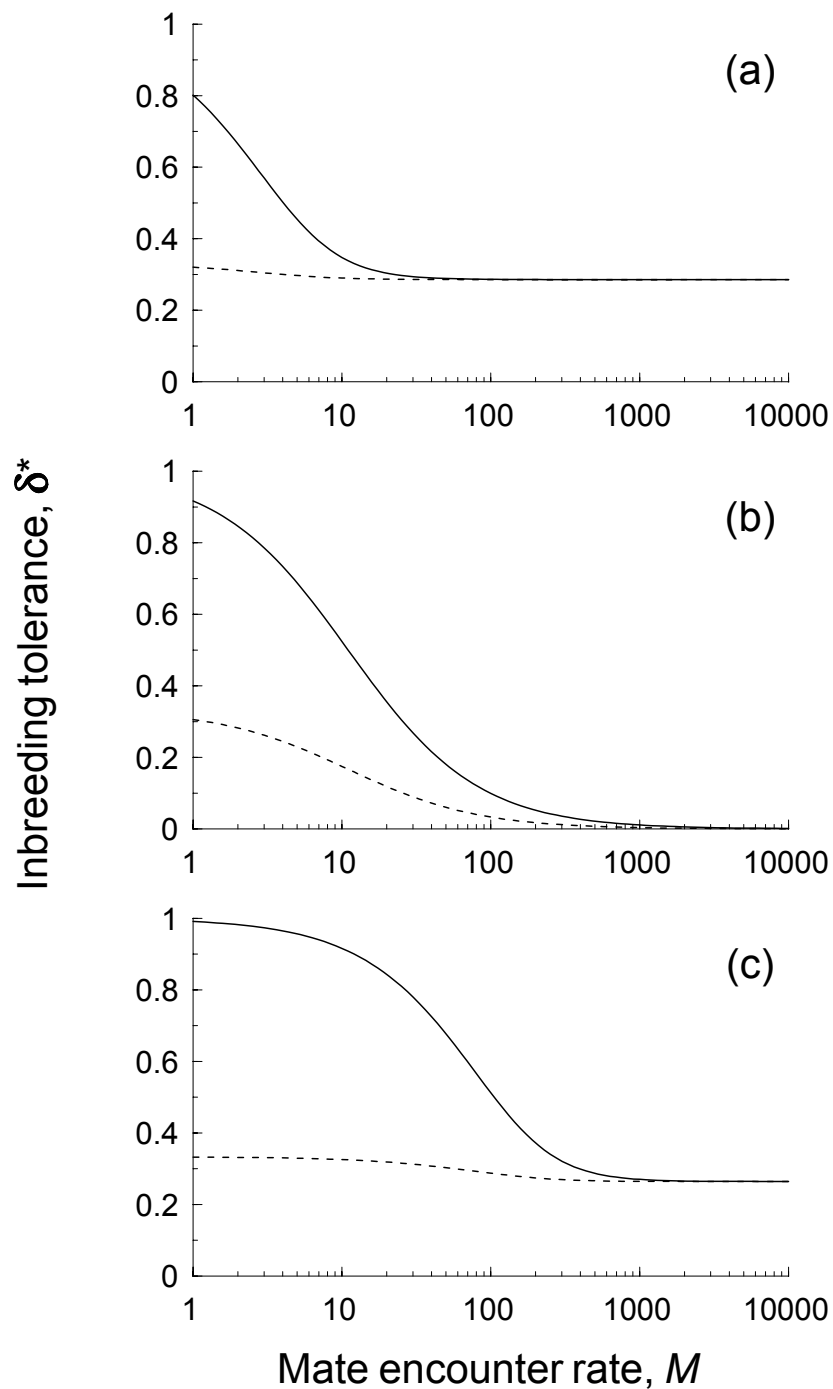
643

644 Fig. 1 Model description. Individuals spend their adult lives alternating between ‘time
 645 in’ and ‘time out’ states, and they encounter potential mates only when in the ‘time in’ state.
 646 See text for further description.



647

648 Fig. 2 Inbreeding tolerance δ^* for different values of ‘time out’ T_w of the opposite sex,
 649 when the choosing sex has time out (a) $T_v = 0.1$, (b) $T_v = 0.01$ (note that the right ends of
 650 figures, where $T_w > T_v$, can be interpreted as male mate choice scenarios). Solid and dashed
 651 lines indicate sequential and simultaneous choice, respectively. Preferences for incestuous
 652 matings are expected to evolve when inbred offspring suffer fitness costs less than δ^* . Other
 653 parameters: $\mu_{Ov} = \mu_{Iv} = \mu_{Iw} = \mu_{Ow} = 1$, $M = 100$, $r = 0.5$.



654

655 Fig. 3 Inbreeding load thresholds δ^* for different values of mate encounter rate M , with
 656 solid and dashed lines indicating sequential and simultaneous choice, respectively, as in Fig.
 657 2. Time in and out parameters: (a) Breeding is much costlier for the choosy sex: $T_v = 0.5$, $T_w =$
 658 0.05 , (b) Parental care duties are shared equally: $T_v = T_w = 0.1$, (c) Breeding is ‘quick’ and
 659 performed many times over the lifetime in both sexes: $T_v = T_w = 0.01$. Other parameters: μ_{Ov}
 660 $= \mu_{Iv} = \mu_{Iw} = \mu_{Ow} = 1$, $r = 0.5$.

661