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WHEN NOT TO AVOID INBREEDING

HANNA KOKKO[1] AND INDREK OTS[2]
[1]*Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Science, University of Helsinki, FIN-00014 Helsinki, Finland*
E-mail: hanna.kokko@helsinki.fi
[2]*Institute of Zoology and Hydrobiology, Tartu University, Estonia*
E-mail: indrek.ots@ut.ee

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

Key words.—Inbreeding, incest avoidance, relatedness, sequential mate choice, sex roles, sexual conflict.

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

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

Whether inbreeding avoidance or optimal outbreeding is considered, arguments are typically based on maximizing the fitness of offspring. However, it has been repeatedly pointed out that mating with one's own kin has an additional—and positive—effect on the parent's inclusive fitness (Bengtsson 1978, Parker 1979, Bateson 1983, Waser et al. 1986, Waller 1993, Lehmann and Perrin 2003). The argument presented below has, in the context of selfing, been presented as early as 1941 by Fisher (1941). To develop the argument, let us first ignore any negative fitness consequences of inbreeding, and consider a female that chooses to mate with her brother instead of another, unrelated male. Also, let us assume that this mating does not involve opportunity costs, or any other costs, to the male. In other words, the brother gains an ''additional'' mating with his sister without this affecting his success with other females. Thus, the female gains direct fitness (number of offspring n) through her offspring, but additionally she gains indirect fitness rn by improving her brother's mating success; total inclusive fitness thus equals $(1 + r)n$. Had she mated with an unrelated male, her inclusive fitness would have remained as n, and mating with kin clearly in this case brought about a substantial benefit.

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

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

THE MODEL

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

The Life Cycle

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

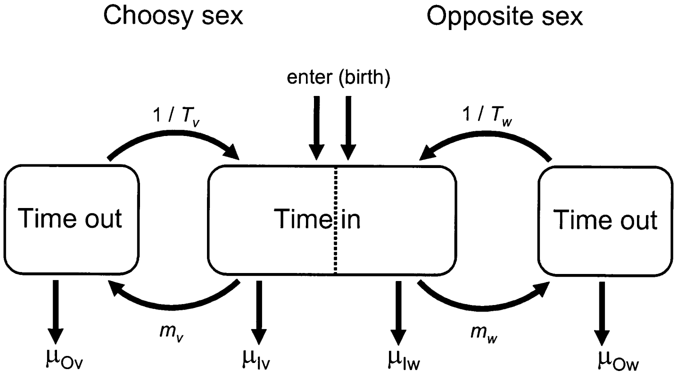

FIG. 1. Model description. Individuals spend their adult lives alternating between ''time in'' and ''time out'' states, and they encounter potential mates only when in the ''time in'' state. See text for further description.

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

We denote the ''time in'' reproductive value of individuals of the choosing sex by v_I, and that of opposite-sex individuals by w_I. The reproductive values during ''time out'' will be v_O and w_O for the choosing and the opposite sex, respectively. Individuals in ''time in'' encounter unrelated potential mates at a rate M if the operational sex ratio is unbiased. The resulting mating rate is $m_v = M\sqrt{\beta}$ for the choosy sex and $m_w = M/\sqrt{\beta}$ for the opposite sex, when the operational sex ratio (males:females) equals β (see Kokko and Monaghan 2001). Mating leads to offspring production, yielding a direct fitness benefit $a(w_I+v_I)$. This corresponds to $2a$ mature offspring of each sex, each related to the parent by 1/2. We constrained our study to values of a that ensure population stability (see Appendix). After mating, both parents enter the ''time out'' state, and its duration can be very different for the two sexes (Figure 1). Denoting the mean duration as T_v for the choosing sex and T_w for the opposite sex, we will often have $T_v > T_w$ because individuals of the choosing sex typically invest more in offspring (Clutton-Brock and Parker 1992). This imbalance will also be reflected in the operational sex ratio, β (see Appendix). Making the time out explicitly modeled takes into account the number of outbred matings forfeited as a result of accepting an inbred mating, which has been shown to be crucial to the question (Waser et al. 1986).

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

Simultaneous Mate Choice

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

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

mate with nonkin: $v_O + rw_I + a(v_I + w_I)$

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

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

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

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

Sequential Choice

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

$$\delta^*_{\text{seq}} = \frac{a(1 + r)(v_I + w_I) - (v_I - v_O) - r(w_I - w_O)}{a(1 + r)(v_I + w_I)}$$

$$= 1 - \frac{(v_I - v_O) + r(w_I - w_O)}{a(1 + r)(v_I + w_I)} \quad (2)$$

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

RESULTS

Inbreeding tolerance is highly context dependent: Simultaneous and sequential mate choice scenarios can show very different values (Figs. 2–3). When an individual has to perform sequential choice, inbreeding avoidance means that both it and its mate lose all current reproductive benefits by not breeding immediately. In particular, if mate encounter rates are low for at least one of the sexes (Fig. 3), this implies that inbreeding should be much more tolerated when mates are encountered sequentially than when the individual can compare two or more mates simultaneously. Under conditions of very high mate availability, the difference between simultaneous and sequential choice vanishes (Fig. 3).

Parker (1979) concluded that when sex roles are well differentiated such that one sex provides all the parental care, the choosy sex should have inbreeding tolerance 1/3 in full-sibling matings ($r = 0.5$), whereas the opposite sex should ''want'' to mate with inbreeding depression reaching as high values as 2/3. Figure 2 supports this and shows how intermediate scenarios with less extreme sex roles link these two cases. Perhaps surprisingly, intermediate cases in terms of

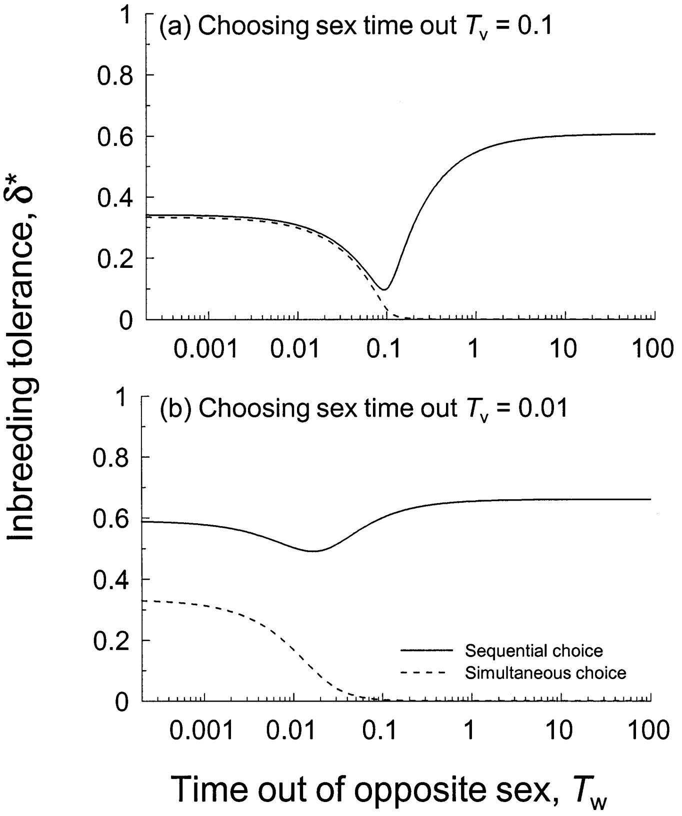

FIG. 2. Inbreeding tolerance δ* for different values of ''time out'' T_w of the opposite sex, when the choosing sex has time out (a) $T_v = 0.1$, (b) $T_v = 0.01$ (note that the right ends of figures, where $T_w > T_v$, can be interpreted as male mate choice scenarios). Solid and dashed lines indicate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

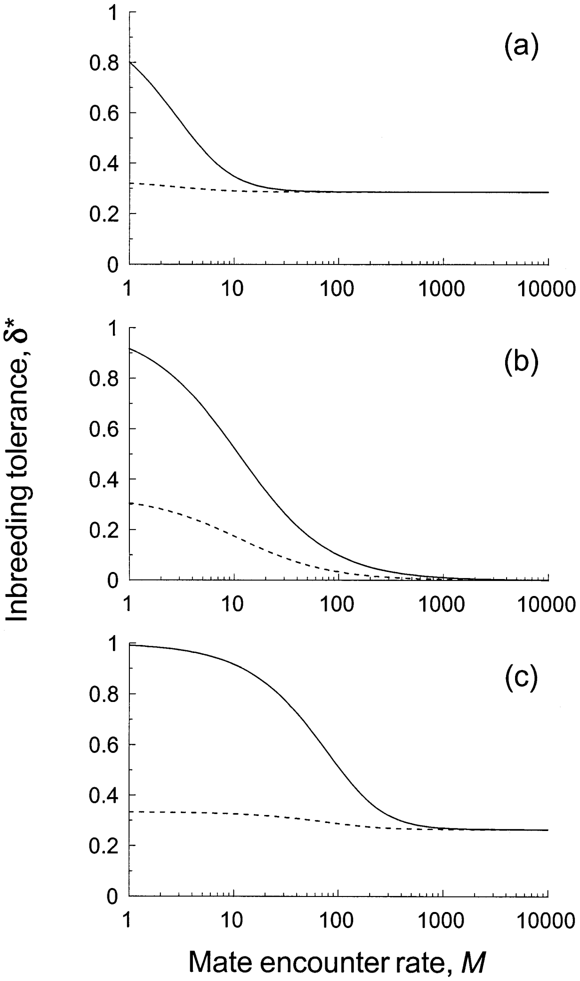

FIG. 3. Inbreeding tolerance δ* for different values of mate encounter rate M, with solid and dashed lines indicating sequential and simultaneous choice, respectively, as in Figure 2. Time in and out parameters: (a) breeding is much costlier for the choosy sex: $T_v = 0.5$, $T_w = 0.05$; (b) parental care duties are shared equally: $T_v = T_w = 0.1$; (c) breeding is ''quick'' and performed many times over the lifetime in both sexes: $T_v = T_w = 0.01$. Other parameters: $\mu_{Ov} = \mu_{Iv} = \mu_{Iw} = \mu_{Ow} = 1$, $r = 0.5$.

sex roles are not necessarily intermediate regarding their inbreeding tolerance. In Figure 2a, the choosing sex has a considerable time out $T_v = 0.1$ (compared to the expected lifespan which equals 1 in all our examples). Toward the left of the figure, the opposite sex has a much shorter time out and can thus be considered a noncaring male; here, the choosy sex prefers to mate incestuously with tolerance $\delta^* = 0.33 \approx 1/3$. Toward the right end of the figure, the opposite sex has a very high time out $T_w = 100$. A very high time out can be interpreted as semelparity: there is virtually no chance that an individual can live to a second breeding attempt. The sex with the lower time out (enabling several breeding attempts for one of the sexes), $T_v = 0.1$, can now be interpreted as being the male. His parental investment is certainly lower than that of the semelparous female, but perhaps sufficiently high to make him choosy (Kokko and Monaghan 2001). The tolerance has now climbed to $\delta^* = 0.66 \approx 2/3$. In between, however, tolerance values do not climb smoothly from 1/3 toward 2/3, but experience a considerable dip where parental investment is roughly equal, $T_v = T_w = 0.1$. At this point of egalitarian parental care, both parents should avoid inbreeding when the fitness costs to offspring exceed 10% (Fig. 2a).

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

Under simultaneous choice, the results are far simpler. Full-sib relatedness $r = 0.5$ leads to values close to the classical threshold $r/(1+r) = 1/3$ when the choosy sex has the higher time out. When the choosy sex is the one that invests less, the threshold drops to close to zero. The results are easy to explain. Consider a species with conventional sex roles, females providing all the parental care, and male reproductive success being limited by their access to females. The first scenario (left sides of Fig. 2a–b, e.g., $T_W < 0.001$) corresponds to a female who has encountered two males, a relative and an unrelated male. She should take into account that the related male probably does not have access to any other females at the moment, and he can gain an additional, cost-free mating (i.e., no opportunity or parental care costs) if she mates with him. Thus, the equations of Parker (1979) apply. The second scenario is described by high values of the opposite-sex time out T_w (e.g., $T_w > 0.1$ in Figs. 2a–b). Since $T_w > T_v$, the interpretation for a conventional species is that a *male* has been lucky enough to locate two receptive females simultaneously: a sister and an unrelated female. Now, the sister is unlikely to have any trouble locating additional mates, thus there is no indirect benefit gained by allowing her to mate right now, and only a cost of producing inferior offspring. Therefore, now the slightest negative consequences of inbreeding should make the male prefer mating with the unrelated female (assuming that she is receptive and willing to accept the current male—as is assumed under our simultaneous choice scenario).

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

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

DISCUSSION

Our results expand on earlier ones (Parker 1979; Lehmann and Perrin 2003) that show that there is a substantial kin-selected benefit to mating incestuously. Our model not only shows that the equation for preferential sibling mating—$\delta < 1/(1 + r)$—should be taken seriously, but also that it often underestimates the magnitude of inbreeding depression that individuals should tolerate. The inbreeding tolerance δ^* is often larger than 1/3 for full-sib matings, particularly if mate choice is sequential rather than simultaneous. The tolerance can even exceed 2/3, the result previously described for males whose reproductive success is solely determined by the number of mating partners (Parker 1979). Yet the empirical literature is almost exclusively focused on inbreeding avoidance.

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

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

Solution 1. Conditions that predict low inbreeding tolerance are the norm

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

A perhaps more likely version of this explanation is that mate choice much more often resembles our simultaneous scenario, which systematically leads to lower tolerance values, than the sequential scenario. If mate choice is a seasonally occurring quick and intense event, it is possible that choosy individuals can during this time compare different potential mates simultaneously or at least in very rapid succession. The predictions of the simultaneous and the sequential scenario indeed become identical when the mate encounter rate M is very high (Fig. 3). Nevertheless, under this scenario the predicted tolerance often saturates near 1/3, rather than zero, and it is therefore an unlikely explanation for a near complete absence of preferences for incestuous matings in the literature.

Solution 2. Models fail to capture reality properly

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

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

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

Solution 3. Inbreeding depression underestimated in nature

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

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

Solution 4. Empirical evidence exists if we look for it

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

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

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

Conclusions

We do not predict that the numerous studies reporting inbreeding avoidance (Pusey and Wolf 1996) are all wrong. Nevertheless, the conditions under which one should expect inbreeding avoidance are stricter than is often assumed. On the other hand, measuring inbreeding depression is not easy, and the real cost of inbreeding may often have been underestimated. There is currently mixed evidence, for example, for the role of relatedness in determining extrapair copulation patterns in birds (Blomqvist et al. 2002; Foerster et al. 2003; Hansson et al. 2004; Kleven et al. 2005; Schmoll et al. 2005). Given the overlap between reported inbreeding depression values in the literature and the large range of inbreeding tolerance values predicted by our model, such a mixed pattern is perhaps the expected one. From an overlap it also follows that the costs and benefits of inbreeding will often roughly balance. Selection pressure to prefer or to avoid kin can therefore become weak, including selection to evolve efficient kin recognition mechanisms. Therefore, lack of inbreeding avoidance that results from an inability to recognize kin does not necessarily mean that the organism is trapped in suboptimal behavior due to a cognitive constraint. Alternatively, a failure to evolve kin recognition can also follow if animals simply do not typically encounter kin in a mating context.

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

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

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APPENDIX

Figure 1 leads to reproductive values as given by the matrix

$$\begin{pmatrix} dv_{\mathrm{I}}/dt \\ dv_{\mathrm{O}}/dt \\ dw_{\mathrm{I}}/dt \\ dw_{\mathrm{O}}/dt \end{pmatrix} = \underbrace{\begin{pmatrix} -\mu_{\mathrm{I}v} + m_v(a-1) & m_v & am_v & 0 \\ 1/T_v & -1/T_v - \mu_{\mathrm{O}v} & 0 & 0 \\ am_w & 0 & -\mu_{\mathrm{I}w} + m_w(a-1) & m_w \\ 0 & 0 & 1/T_w & -1/T_w - \mu_{\mathrm{O}w} \end{pmatrix}}_{\mathbf{A}} \cdot \begin{pmatrix} v_{\mathrm{I}} \\ v_{\mathrm{O}} \\ w_{\mathrm{I}} \\ w_{\mathrm{O}} \end{pmatrix} \tag{A.1}$$

Here, for example, the first row results from noting that dv_{I}/dt, the change in reproductive value for a female in the ‘‘time in’’ state, depends on the mating rate m_{v}, and on the death rate μ_{Iv}. Mating leads to direct fitness increase $a(v_{\mathrm{I}} + w_{\mathrm{I}})$, but also to the replacement of the individual's own ‘‘time in’’ reproductive value v_{I} by the ‘‘time out’’ value v_{O}. The net change due to mating is therefore $m_{\mathrm{v}}\ [(a-1)v_{\mathrm{I}} + v_{\mathrm{O}} + aw_{\mathrm{I}}]$, and due to death, $-\mu_{\mathrm{Iv}}v_{\mathrm{I}}$ (for a mathematical justification of this method, see Härdling et al. 2003). These are expressed in matrix format in equation (A1). The values of m_{v} depend on the operational sex ratio β as $m_{\mathrm{v}} = M\sqrt{\beta}$ (see main text). β is calculated according to equation (3) in Kokko and Monaghan (2001), where the model population follows an equivalent life cycle. The value a is chosen such that each mature individual of the choosy sex produces, on average, one mature offspring of the same sex, which implies a stable population regulated by the probability that a newly born offspring recruits into the population as a mature adult. From equation (A.1) it follows that a newly matured individual of the choosy sex reproduces, on average, $m_{\mathrm{v}}(1/T_{\mathrm{v}} + \mu_{\mathrm{Iv}})/(\mu_{\mathrm{Ov}}/T_{\mathrm{v}} + \mu_{\mathrm{Iv}}(m_{\mathrm{v}} + \mu_{\mathrm{Ov}}))$ times before death, thus a is given by the equation $2a = [m_{\mathrm{v}}(1/T_{\mathrm{v}} + \mu_{\mathrm{Iv}})/(\mu_{\mathrm{Ov}}/T_{\mathrm{v}} + \mu_{\mathrm{Iv}}(m_{\mathrm{v}} + \mu_{\mathrm{Ov}}))]^{-1}$.

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 matrix (for a justification see, e.g., Härdling et al. 2003). The associated eigenvalue gives the relationship between the values v_{I}, v_{O}, w_{I}, and w_{O}. In practice, these eigenvalues are calculated numerically, as the analytical solution is unwieldy.