



# An agent-based model of the female rivalry hypothesis for concealed ovulation in humans

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**After half a century of debate and few empirical tests, there remains no consensus concerning why ovulation in human females is considered concealed. The predominant male investment hypothesis states that females were better able to obtain material investment from male partners across those females' ovulatory cycles by concealing ovulation. We build on recent work on female competition to propose and investigate an alternative—the female rivalry hypothesis—that concealed ovulation benefited females by allowing them to avoid aggression from other females. Using an agent-based model of mating behaviour and paternal investment in a human ancestral environment, we did not find strong support for the male investment hypothesis, but found support for the female rivalry hypothesis. Our results suggest that concealed ovulation may have benefitted females in navigating their intrasexual social relationships. More generally, this work implies that explicitly considering female-female interactions may inspire additional insights into female behaviour and physiology.**

In some non-human primate species, ovulation is clearly revealed by overt indications of female ovulation<sup>1</sup>. For example, female chacma baboons have red, swollen genitals near peak fertility; these swellings are dramatic, with maximal swelling increasing a baboon's body weight by up to 14%<sup>2,3</sup>. What adaptive benefits, if any, might human females have gained from concealing ovulation?

After half a century of debate and few empirical tests, there is still no consensus about why ovulation in human females is largely concealed<sup>4–20</sup>, although most existing accounts, proposed in the latter half of the twentieth century, tend to focus on the benefits females may have gleaned by concealing ovulation from males. For example, the predominant account—the male investment hypothesis—holds that by concealing cues of ovulation, females were better able to obtain investment from male partners across those females' ovulatory cycles.

Here, we propose and test an alternative account—the female rivalry hypothesis—which posits that females may have avoided costs of being the target of costly aggression from other females by concealing ovulation cues. We use a spatial agent-based model to test the hypothesis that females who concealed ovulation from other females avoided aggression under circumstances when females perpetrated aggression towards attractive and/or ovulating females. This female rivalry hypothesis is consistent with a growing body of work suggesting that females are active and purposeful agents who enact intrasexual aggression in the course of mating competition, and also that females can preferentially and selectively aggress against ovulating mating rivals<sup>21–32</sup>.

Many scholars in this area assume that ancestral human females experienced a loss of overt signals/cues of ovulation during our evolutionary history, and thus focus on potential adaptive explanations for why this might have occurred (most of the references

cited above, as well as refs. <sup>33,34</sup>) and why women's ovulation is relatively concealed. However, this view is not shared by all scholars. For example, one argument<sup>1</sup> holds that ancestral human females did not evolve concealed ovulation because ovulation was already concealed in humans' direct ancestors (that is, they did not possess sexual swellings; see also refs. <sup>15,35</sup>). Another view is that ancestral females possessed more slight, rather than particularly overt, ovulatory swellings, given the presence of such swellings in the Old World monkey family<sup>14,36</sup>. There is currently no complete scientific consensus about exactly when concealed ovulation arose. In line with prevailing views, we assume that ancestral females possessed at least some overt signals/cues of ovulation, which have become relatively concealed over time<sup>34</sup>. Moreover, relatively concealed does not imply that cues of women's ovulation are now completely concealed. Humans have retained some perceptible cues of ovulation, even if those cues are not overt or necessarily perceptible within conscious awareness<sup>37–39</sup>. Abundant evidence suggests that social perceivers are able to detect and adaptively respond to ovulation cues, including those from odour<sup>40</sup>, voice<sup>39,41</sup> and physiognomy<sup>37,42</sup>.

Consistent with much of the existing literature, then, we begin with the assumption that human females evolved relatively concealed ovulation. However, in contrast with the existing literature, which has focused largely on the benefits that females might have gained by concealing ovulation from males, we propose that females might have gained benefits by concealing ovulation from other females. Our hypothesis is built on a modern, theoretically informed view of females as active, purposeful agents who both perpetrate and thus must also avoid intrasexual aggression. We hypothesize that concealing ovulation may have provided fitness benefits by allowing females to avoid aggression from other females. We test predictions derived from the female rivalry hypothesis using an

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agent-based model of mating behaviour and paternal investment in the human ancestral environment. We also test predictions derived from the prevailing account—the male investment hypothesis.

The male investment hypothesis is the most widely cited hypothesis regarding the adaptive benefits of concealed ovulation. For example, Alexander and Noonan's<sup>4</sup> male investment hypothesis has been cited nearly twice as often as Hrdy's infanticide account<sup>10</sup>, more than twice as often as either Burley's<sup>6</sup> or Bensch's and Thornhill's<sup>5</sup> hypotheses and roughly 20 times as often as Spuhler's<sup>16</sup> by-product account, even as all accounts were published in 1979. Hrdy's<sup>10</sup> article focused on infanticide in animals and is widely cited for content unrelated to the evolution of concealed ovulation so we included in this number only citing articles that also included the word ovulation anywhere in the article. The male investment hypothesis posits that females who concealed ovulation were better able to obtain material investment from male partners, not only at peak fertility but also across the ovulatory cycle. According to this account, males who could not tell whether a female was ovulating had no choice but to invest in the female throughout her cycle to increase paternity certainty, with investment presumably increasing the fitness of the female and her offspring. Among the Ache, for example, father presence and investment has indeed been shown to increase offspring survival by up to 35%<sup>43</sup>. According to this account, then, consistent male investment in females who concealed ovulation would bolster those females' reproductive success<sup>4</sup>.

There have been substantial challenges to this male investment hypothesis<sup>10,34,36</sup>. For example, contrasting with the paternity certainty functions of males' investment, Hrdy suggested that concealed ovulation benefits females by allowing them to confuse paternity; by mating throughout the cycle, more numerous males might believe that they could be the potential fathers, which could reduce the likelihood of infanticide and thus increase female fitness<sup>10</sup>. Another potential challenge is that, compared with females revealing ovulation, females concealing ovulation might be less attractive to males precisely because they are not advertising their current fertility status, implying that males might have invested less in concealing females. One potential resolution to this is for females to conceal ovulation, not through suppressing ovulation cues, but rather by presenting cues of fertility, and/or perhaps receptivity, throughout the cycle. Along these lines, the extended sexuality hypothesis proposes that females are receptive throughout the ovulatory cycle in order to enhance investment from males<sup>34,44</sup>.

We present an alternative—although not necessarily mutually exclusive—hypothesis regarding the adaptive benefits of concealing ovulation for females: the female rivalry hypothesis.

Existing theories were proposed at a time when it was largely assumed that men (more than women) were competitive and women (more than men) were choosy. However, recent work has made it clear that female aggression and competition are important in mating and other social contexts<sup>45–49</sup>. Moreover, female intrasexual aggression can be costly, disrupting valuable social ties and possibly even affecting the ability to conceive, carry and rear offspring<sup>1,21,23,28,50–59</sup>. This is true even as the types of aggression typically enacted between women are less overt; compared with males, who use both physical (for example, punching) and non-physical tactics (for example, gossip), human females strongly prefer to enact intrasexual aggression via the latter—using reputation denigration, gossip and social exclusion—and some non-human primate females are also thought to engage in more social exclusion than male conspecifics<sup>23,28,30,46,47,60</sup>. Such female competition can effectively decrease the desirability of targets in the eyes of both prospective mates and cooperative partners in multiple ways<sup>23,28,47–49</sup>. For example, women's derogatory comments about a female target's appearance can cause men to view that target as less physically attractive<sup>61</sup>. Other work has demonstrated a range of negative consequences associated with female intrasexual victimization, including increases in negative

evaluation by prospective cooperative partners and negative effects on victims' health and wellbeing<sup>47,62</sup>.

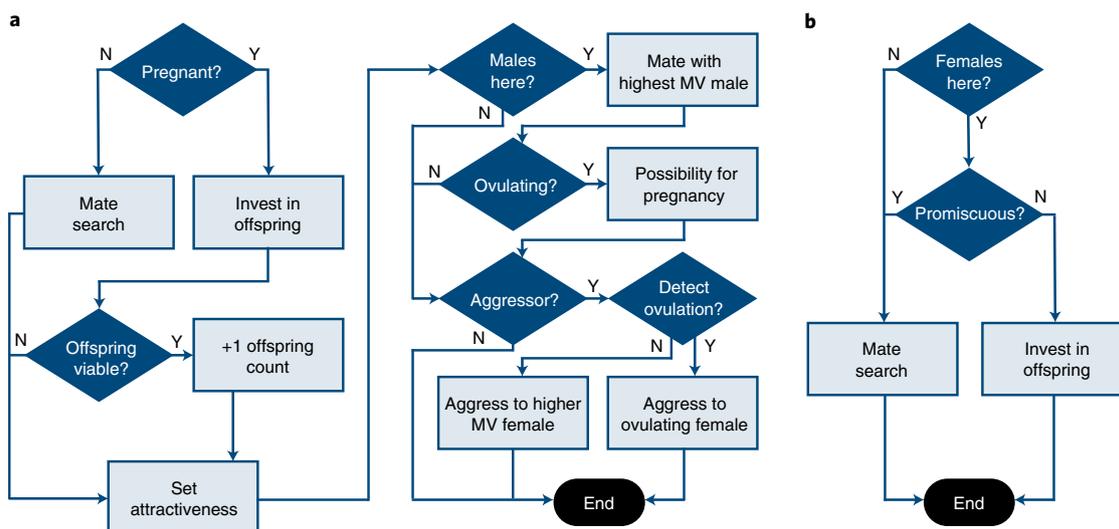
Moreover, female intrasexual aggression is not indiscriminate. Females often preferentially and selectively direct their aggression towards rivals who are competitive for desirable mates<sup>23,28,63–65</sup>. This means that higher mate-value females (for example, those deemed most physically attractive and/or sexually desirable to men) are more likely to be targets of female intrasexual aggression<sup>23,28,66,67</sup>. In one study, for example, women's physical attractiveness increased their odds of incurring indirect aggression (whereas men's physical attractiveness decreased it)<sup>66</sup>. As another example, wearing red makes women more attractive to men<sup>68</sup>, and women may be more aggressive towards women wearing red<sup>69</sup>.

Ovulation status may also influence whether a female is a likely target of intrasexual aggression. A female rival may be seen as a greater threat when ovulating because: (1) male prospective mates might be more attracted to her when she is ovulating<sup>38,39,41,42,70–78</sup>; and (2) during ovulation, that female might have greater mating desires, engage in more mate-attracting and mate-pursuing behaviour and also enact in more intrasexual competition<sup>79–104</sup>. In line with this, laboratory studies show that both men and women are able to detect and respond to subtle and non-conscious cues of women's ovulatory status<sup>37,42,64,105</sup>, with female participants often reporting less favourable feelings towards ovulating versus non-ovulating women<sup>24,106</sup>. Furthermore, women engage in more mate-guarding behaviour and intrasexual aggression when potential rivals are depicted at high- rather than low-fertility points of their cycles<sup>53,64,107</sup>. In contrast, men, and especially male romantic partners, may engage in more mate guarding (but less physical aggression) towards ovulating partners<sup>107</sup>.

Together, these findings suggest that one adaptive benefit of concealed ovulation may have been the avoidance of costly intrasexual victimization, thereby allowing for higher reproductive fitness among females concealing ovulation than females revealing ovulation. Here, we create an agent-based model of an ancestral environment in which we test both the male investment hypothesis and this female rivalry hypothesis. We do this by measuring the success of female agents who conceal ovulation (concealers) or reveal ovulation (revealers) in different model circumstances.

Behaviour does not fossilize; it is impossible to gather data on the social interactions and mating patterns of human ancestors, making agent-based models a useful tool for investigating the evolutionary viability of various strategies and decision rules. We used a spatial agent-based model because it serves as a realistic model of many aspects of the ancestral mating environment. This approach also allows us to specify the behaviour of both sexes, making it consistent with what we know about human mating behaviour. We developed and parameterized this model based on extensive data from theoretical and empirical work in small-scale societies dealing with mate choice, intrasexual competition, female reproduction, parental investment, human ovulation cycles, interbirth intervals and other reproductive and social parameters (see Supplementary Table 1).

In the model, male and female agents can move around to form pairs, mate, conceive and invest in offspring together (Fig. 1). In the model, both males and females face a fundamental trade-off between mate search and offspring investment: during each time step (corresponding to one day), we assume that individuals can either search for mates or invest in offspring. Males approach females with high attractiveness. Female attractiveness is an aggregate of mate value and ovulatory status (if revealed), and attractiveness could potentially be reduced as a result of aggression from other females. After mating, males stay with females based on the male's promiscuity parameter, which we systematically varied, as described below. Pregnancy can result from mating if that mating occurred during the female's fertile window. Males that stay with their mate provide resources at each subsequent time step while they stay. Males that



**Fig. 1 | Flowchart summarizing the schedule for our agent-based model for both female and male agents. a, b,** Flowcharts for female (a) and male agents (b). See Supplementary Materials for detailed ODD protocol. MV, mate value.

do not stay and invest (promiscuous males) continue searching for attractive partners and leave their current mate if they find a more attractive female within the search radius.

Males approach females with the highest attractiveness within their search radius. Females have two potential strategies: they are either ovulation concealers (not exhibiting any cues of ovulation and maintaining the same level of physical attractiveness throughout the cycle) or ovulation revealers (exhibiting ovulation cues and receiving a 25% increase in their overall attractiveness when ovulating). There are possible discrepancies between concealer and revealer average attractiveness, as revealers have higher attractiveness during ovulation; thus, we ran two versions of each of our three experiments. In one version, revealers' increase in mate value during ovulation was offset by lower attractiveness across the rest of the ovulatory cycle, ensuring equal average attractiveness across each cycle for both strategies. In the other version, which provided an even stronger test of our hypothesis, revealers received an attractiveness increase during ovulation but did not suffer a concomitant decrement in attractiveness during the rest of the ovulatory cycle.

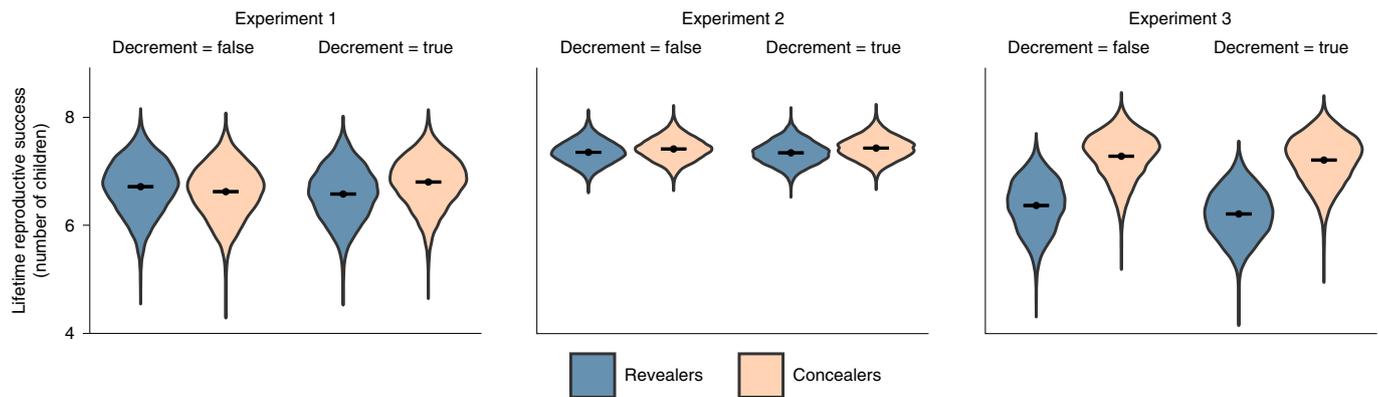
Among revealers, being in an ovulatory state increases attractiveness, so for this population of females, attractiveness is associated with a higher probability of getting pregnant. Among concealers, attractiveness is not affected by ovulatory status and is therefore not associated with a higher probability of becoming pregnant. However, even for concealers, females with higher attractiveness will be more likely to attract a mate.

As discussed earlier, human females are known to aggress against ovulating and/or physically attractive rivals, and this aggression can have negative effects on victims<sup>53,108–113</sup>. The key question we explored in this model is whether, when females are able to inflict costs on rivals (through decreasing the attractiveness of those rivals), those females who conceal ovulation have a fitness advantage over those females who do not conceal ovulation. This is not to imply that perpetrators are consciously and/or intentionally levying costs on possible victims. In the experiments that included intrasexual aggression, females directed their aggression either at females with higher attractiveness in general (experiment 2) or specifically at females displaying ovulation cues (experiment 3). Because aggression decreases the attractiveness of female rivals, this could lead to indirect fitness costs for those rivals, as they would be less likely to

be chosen as mates, and therefore less likely to attract an investing mate and/or become pregnant. In the model, we did not explore whether engaging in aggression provided a benefit for female perpetrators, as this was not our central question; however, females who aggressed against others may have experienced indirect benefits from reduced competition from rivals for mating opportunities and parental investment.

Each time step in the model represents one day, and during each day, every individual (whether male or female) faces a trade-off between mate search and offspring investment. If a male does not have a current mate and/or if they are promiscuous, that male engages in mate search. If a female is not pregnant, she engages in mate search. Males and females of both types search for mates by moving in the simulated spatial world. Males go to the patch within their search radius with the most attractive female, and females choose the male mate on their current patch who is highest in attractiveness. Movement is the mechanism for mate search, and because mate search trades off with parental investment, males and females who are investing in offspring stay in one physical location. This biparental investment can be observed as pairs who are in the same spatial location for multiple time steps as the model runs.

Occasionally, when the model is running at full speed, a halo will appear in the model where an attractive female appears encircled by promiscuous males. This happens because promiscuous males spend only one time step (day) with the female before searching again, and they do not stay with a partner even if that partner is the most attractive female within their search radius. Promiscuous males who are near attractive females will sometimes move to the attractive female in one time step, mate with that female if she chooses them, and then leave her in the next time step to search, only to return to that same mate in the following time step because she is still the most attractive female in the search radius. This halo of promiscuous males can also occur when several attractive females happen to be in the same spatial location in the model. This effect appears to occur more often around concealers than revealers. Another effect that can be seen in the model is that investing males who have selected a particular female as a mate can sometimes appear to follow their female mate. This occurs because females who are not pregnant continue to move, whereas males who are not promiscuous will update their spatial location to match that of their female mates.



**Fig. 2 | Lifetime reproductive success of revealers and concealers after 10,000 time steps in the model.** Violin plots summarizing the results of 10,000 independent model runs. Central points show mean values and whiskers represent standard errors, but the standard errors are so small that they overlap and form a single bar. Revealers are shown in blue and concealers are shown in beige. When no aggression is possible (experiment 1), concealers only outperform revealers with a small effect size if revealers experience an attractiveness decrement during non-fertile days (decrement = true). When aggression towards attractive rivals is possible (experiment 2), concealers have higher reproductive success than revealers, with small effect sizes. When aggression towards ovulating females is possible (experiment 3), concealers have higher reproductive success than revealers, with large effect sizes. See Supplementary Table 4 for inferential statistics.

Offspring are not explicitly created as new individuals in this model, but rather are represented as state variables in the female parent (see Supplementary Table 2). This allows us to measure lifetime reproductive success of females over a typical reproductive window.

In all, we modelled three experiments to examine the lifetime reproductive success for revealers and concealers. Experiment 1 examined lifetime reproductive success when there was no female aggression (our control condition, and also a model that allowed us to test predictions derived from the male investment hypothesis). Experiment 2 began to test the female rivalry hypothesis, as females in this model aggressed against the most attractive nearby females (but not specifically against ovulating females). Experiment 3 further tested the female rivalry hypothesis, as females in this model aggressed against nearby ovulating females. As noted above, because of the possible discrepancies between concealer and revealer average attractiveness, we ran two versions (conditions) of each of these three experiments: one where revealers gained increased attractiveness during ovulation that was then offset by decrements in attractiveness during the rest of the ovulatory cycle (decrement condition); and one where revealers simply gained increased attractiveness during ovulation, with no related offset (no decrement condition). We used established Cohen's  $d$  thresholds<sup>114</sup> to compare effect sizes across experiments and conditions ( $d < 0.2$  = negligible;  $0.2 < d < 0.5$  = small;  $0.5 < d < 0.8$  = medium;  $d > 0.8$  = large).

In addition to measuring reproductive success, we also measured paternal investment, but because these results were nearly identical to those for lifetime reproductive success (Extended Data Fig. 1), we present the paternal investment results in the Supplementary Information.

Data, code and pre-registration for this study can be found at <https://osf.io/c5pq7/>.

## Results

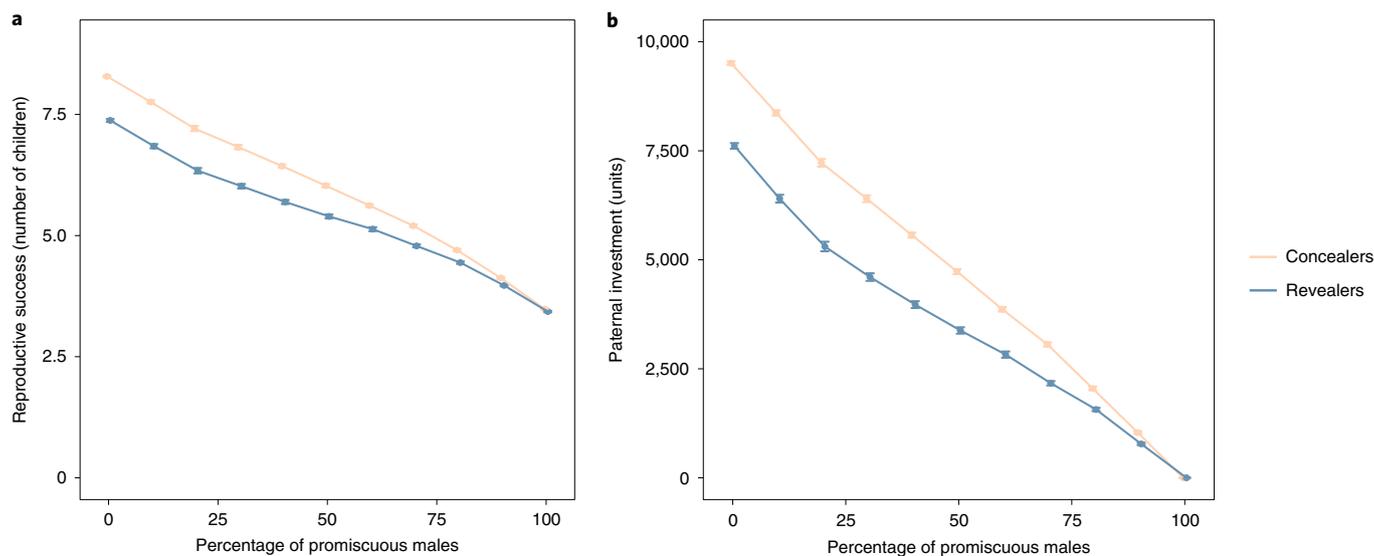
In experiment 1, we assessed the lifetime reproductive success of concealers and revealers in the absence of female aggression (our control condition, and also a model that allows tests of predictions derived from the male investment hypothesis). This condition reflected traditional thinking at the time that the male investment hypothesis was proposed (that is, it did not explicitly acknowledge female intrasexual mating competition<sup>4,48,49</sup>). When revealers

received an attractiveness decrement during non-ovulatory periods, concealers had significantly higher lifetime reproductive success ( $M = 6.80$  children) than revealers ( $M = 6.58$  children) with a small effect size (paired  $t$ -test,  $t(9,999) = -37.29$ ;  $P < 0.001$ ; Cohen's  $d = 0.46$ ; 95% confidence interval (CI) =  $-0.23$  to  $-0.21$ ), providing some support for the male investment account (Fig. 2). However, when revealers received no attractiveness decrement during non-ovulatory periods, they had significantly higher lifetime reproductive success ( $M = 6.71$  children) than concealers ( $M = 6.62$  children) with a negligible effect size ( $t(9,999) = 14.58$ ;  $P < 0.001$ ; Cohen's  $d = 0.19$ ; 95% CI =  $0.08$  to  $0.10$ ). This result is inconsistent with the male investment hypothesis. We found these same patterns for paternal investment (see Supplementary Information).

In the next experiments, females were able to aggress against other females, imposing costs on victims. If a female was the target of aggression, her attractiveness was temporarily reduced. (As noted above, reduction in attractiveness is one outcome of reputation denigration, a common form of intrasexual aggression among human females<sup>61</sup>.) In experiment 2, we allowed female agents to aggress towards the most attractive nearby females. In experiment 3, we allowed female agents to aggress towards nearby females displaying ovulation cues. This allowed us to distinguish between two scenarios in which concealed ovulation might provide a benefit: one in which females aggress towards generally attractive females (and so concealers benefit by not appearing as attractive); and another in which females aggress towards ovulating females specifically (and so concealers get the benefit of avoiding aggression by not showing cues of ovulation).

When females aggressed towards the most attractive females (experiment 2), concealers had significantly higher lifetime reproductive success than revealers (Fig. 2). This held both when revealing females experienced a decrement in attractiveness (concealers: mean ( $M$ ) = 7.43 children; revealers:  $M = 7.34$  children;  $t(9,999) = -27.89$ ;  $P < 0.001$ ; Cohen's  $d = 0.41$ ; 95% CI =  $-0.09$  to  $-0.08$ ) and when they did not (concealers:  $M = 7.41$  children; revealers:  $M = 7.35$  children;  $t(9,999) = -19.52$ ;  $P < 0.001$ ; Cohen's  $d = 0.29$ ; 95% CI =  $-0.07$  to  $-0.06$ ). These effect sizes were small. Findings for paternal investment replicated those for lifetime reproductive success.

In experiment 3, which was our primary test of the female rivalry hypothesis, females aggressed towards other females who exhibited



**Fig. 3 | Effects of varying the percentage of promiscuous males in the population. a, b**, For both reproductive success (**a**) and paternal investment (**b**), the advantage of concealers is reduced when more males in the population are promiscuous. When 100% of males are promiscuous, there is no paternal investment and no difference between concealers and revealers. The data points represent means across 100 independent model runs per parameter value. The error bars represent standard errors. See Supplementary Table 6 for inferential statistics.

cues of ovulation. Supporting predictions, concealers achieved significantly higher lifetime reproductive success than revealers (Fig. 2). This held both when revealers received an attractiveness decrement (concealers:  $M=7.21$  children; revealers:  $M=6.21$  children;  $t(9,999)=-329.99$ ;  $P<0.001$ ; Cohen's  $d=2.19$ ; 95% CI =  $-1.00$  to  $-0.99$ ) and also when they did not (concealers:  $M=7.28$  children; revealers:  $M=6.37$  children;  $t(9,999)=-289.64$ ;  $P<0.001$ ; Cohen's  $d=1.97$ ; 95% CI =  $-0.92$  to  $-0.91$ ). In contrast with experiments 1 and 2, these effect sizes were large. Findings for paternal investment again replicated those for lifetime reproductive success.

To further investigate the conditions under which this possible fitness advantage for concealers would hold, we varied several model parameters in new simulations while keeping constant all other experiment 3 parameters. First, we found that this pattern of results was robust to changes in the attractiveness multiplier for revealers during fertile periods (that is, how much more attractive revealers became during ovulation), as well as the radius of competition for females, the radius of mate search for males, the required offspring investment units, population size, the proportion of females in the population, the proportion of concealers to revealers and the size of the lattice (Extended Data Figs. 2–4).

More notably, we also found that concealers achieved higher reproductive success (and accumulated more paternal investment) than revealers when the following conditions were met: (1) some males in the population were not promiscuous; (2) intrasexual aggression was damaging to female victims and these victims healed from this aggression slowly; and (3) perpetrating aggression was relatively low cost. These sensitivity analyses indicate boundary conditions for our results.

When 100% of males in the population were promiscuous (that is, all males engaged in mate search exclusively and did not invest in offspring), neither concealers nor revealers received any paternal investment (Fig. 3b) and so there was no difference between concealers and revealers in our primary outcome measure of reproductive success (Fig. 3a).

The benefit for concealers over revealers also disappeared when females healed very quickly from aggression (Extended Data Fig. 5), presumably because the costs of receiving aggression are low and so

there is not much benefit from concealing ovulation to avoid mild aggression. Additionally, compared with revealers, concealers had higher reproductive success (and paternal investment) only when there was some cost of being aggressed against and the cost of perpetrating aggression was low (Extended Data Fig. 6). If the cost of being victimized is zero, there is no advantage to concealing ovulation and avoiding that aggression, so there is no difference between concealers and revealers. If the cost of perpetrating aggression is too high (greater than one unit of investment, the daily budget of an agent), these high costs appear to drown out the differences between concealers and revealers.

These social conditions favouring concealers (that is, lower promiscuity, high cost of being aggressed against and low cost of perpetrating aggression) are perhaps likely to have been met in ancestral environments. First, not all males are promiscuous, and some are very low in promiscuity<sup>115–119</sup>. Second, female intra-sexual aggression can impose high and long-lasting costs on targets<sup>108–110,120</sup>, and by adopting typically covert and non-physical tactics, female aggressors are thought to be able to avoid the costs associated with perpetrating more overt and physical acts of aggression<sup>21,23,26,30,47,51,121,122</sup>.

## Discussion

We tested two hypotheses—the male investment hypothesis and the female rivalry hypothesis—regarding the proposed adaptive benefits that females might have gained by concealing versus revealing ovulation. In our test of the male investment hypothesis, which was also the control condition, featuring no female–female aggression, we found mixed support. When female aggression was not possible, ovulation-concealing females received a benefit (in terms of increased reproductive success and paternal investment) only when ovulation-revealing females had an additional decrement in their mate value during non-ovulatory times; otherwise, revealers had higher reproductive success than concealers. In contrast, when female–female aggression was possible, concealers received less aggression than revealers (Extended Data Figs. 7 and 8) and concealers also consistently outperformed revealers, supporting the female rivalry hypothesis and its suggestion that the adaptive benefits females might have gained by concealing versus revealing

ovulation could be linked to the avoidance of victimization from female intrasexual aggression.

Although we did not find clear support for the male investment hypothesis, our results suggest that the male investment hypothesis is more viable if ovulation-revealing females experience a decrement in attractiveness from their baseline mate value during infertile times. Our results also suggest that male investment may have played an important role in the evolution of concealed ovulation in relation to the female rivalry hypothesis. When male investment was zero (Fig. 3b), there was no difference between concealers and revealers in terms of reproductive success (Fig. 3a). This shows that male investment may indeed be important for the advantage that concealers have, but through a different mechanism than was previously proposed in the male investment hypothesis<sup>4</sup>. That is, male investment may be important not necessarily because males selectively invest in concealers, but because revealers may be more likely targets of female aggression (for example, reputation denigration), which might subsequently reduce male investment.

One of the limitations of the present model is that male strategies were programmed to be relatively simple. For example, we assumed for modelling purposes that males were either promiscuous (investing only in mate search) or not promiscuous (switching to investing in offspring after mating)<sup>115–119</sup>. However, in the real world, male mating and parental investment strategies are more nuanced and complex<sup>123–125</sup>. Similarly, the existing work on the male investment hypothesis<sup>4</sup> does not specify the exact algorithms of male investment decision-making. Thus, a promising area for future work may be to use both models and experiments with human subjects to better understand the decision rules underlying male investment decisions; these decision rules can then be used to create models testing their viability.

Another limitation of this model is that we relied on existing empirical work to parameterize it, but not all parameters are equally well supported. In particular, there is little empirical work that directly measures male promiscuity in the way it was operationalized here. In the range we explored, we found relative advantages for concealers over revealers at low male promiscuity. As promiscuity increased, there remained consistent yet diminishing advantages for concealers over revealers. We used a combination of data on infidelity<sup>115,126,127</sup>, nonpaternity<sup>128,129</sup> and polygyny<sup>130–132</sup> (additional data from D.P. Schmitt, personal communication, December 29, 2019) to establish a range of male promiscuity rates (1–35%); admittedly, none of these constructs was exactly the same as the way promiscuity was operationalized in the model (that is, in the model, males were either non-promiscuous (meaning they invested in offspring after finding a mate) or promiscuous (continuing to engage in mate search indefinitely and never engaging in paternal investment)). As additional empirical work is published on male promiscuity, this model can be re-parameterized to explore other ranges of male promiscuity.

Our experiments did not test every hypothesized adaptive benefit of concealed ovulation present in the current literature<sup>6,14,33</sup>. We also did not model evolutionary dynamics; rather, we focused on testing specific hypotheses regarding the possible adaptive benefits of concealed ovulation. There may also have been several distinct evolutionary pressures leading to selection for concealed ovulation in humans. Our findings do not imply that the presence of selective or impactful female aggression was the sole factor rendering concealed ovulation beneficial. For example, in some other primates (for example, bonobos), there exist both costly female intrasexual aggression and also overt cues of ovulation<sup>133</sup>, suggesting that female intrasexual aggression alone does not necessarily cause ovulation to become concealed. To understand the contribution that avoiding female aggression may have played in the phylogeny of concealed ovulation, future work may benefit from systematically cataloguing the presence and modes of female intrasexual competition as well

as the presence and extent of ovulatory cue display across a range of non-human primates.

With respect to the debate about whether humans lost cues of ovulation, these modelling results show one potential adaptive benefit of concealing ovulation cues. During ovulation, female reproductive hormones change drastically, and these hormones have effects throughout the body, some of which may be detectable to conspecifics. This means that some ovulation cues may have originally arisen as byproducts of women's reproductive functioning, independent of any sexual swellings that might have been present in ancestral females. Males who could detect these cues could have derived a substantial evolutionary benefit through increased reproductive success. Despite the potential fitness benefits that males could gain from detecting ovulation cues, ovulation cues in modern humans remain subtle and difficult to detect by both sexes. One potential explanation for why women's ovulation cues may be relatively concealed is that female bodies may have evolved to actively conceal them. Concealment is nonetheless imperfect, perhaps because complete concealment (for example, dramatically reducing oestrogen levels) could compromise the physiology that enables reproduction<sup>134</sup>. The female rivalry hypothesis provides one potential explanation for the benefits females may have gained by concealing ovulation.

Although we cannot answer questions about the evolutionary phylogenetics of concealed ovulation, the present work does show that socioecological pressures from other females can potentially influence the evolution of female physiology and reproductive communication. This suggests that future theory and research on the evolution of female reproduction and mating behaviour should take into account female–female interactions in addition to typically foregrounded male–female interactions. Without doing so, it may be tempting to assume that certain aspects of female reproductive physiology (for example, concealed ovulation) evolved because of the benefits that come from interactions with males, or even for the benefit of males (for example, to enhance paternity certainty), without considering alternative explanations that may be rooted in the costs and benefits of female–female interactions. In the present model, we have shown that protection from female aggression provides a potential explanation for the adaptive benefits of concealed ovulation in human females.

## Methods

**Model design.** We developed an agent-based model to investigate the evolutionary viability of concealed versus revealed ovulation in females under different conditions, which allowed us to test whether concealed ovulation could provide reproductive benefits when females are able to detect and aggress against ovulating rivals. The model represents a human mating environment in which male and female agents can move around to form pairs, mate and conceive/invest in offspring together. This model is parameterized based on extensive theoretical and empirical work on mate choice, intrasexual competition, female reproduction, parental investment, human ovulation cycles, interbirth intervals and other reproductive factors (Supplementary Table 1).

Space and time are modelled discretely. In each time step, agents and patches (lattice locations) execute the commands described in the schedule. One time step is equivalent to a single day (because this is short enough to be a realistic time scale on which agents are changing partners and making trade-offs between mating and offspring investment, and not so short that it would be computationally intractable). Space is represented as discrete locations in a two-dimensional 21 × 21 lattice. Movement within this lattice is determined by mate search decision rules (see below). In this model, movement in space is meant to simulate the movement associated with mate search. Space in the model is not meant to explicitly represent physical sites, but instead movement represents being in a state of searching for mates. Staying in one location represents being in a state of investing in parental care (rather than mate search). Agents could move around the lattice freely, similar to movement in a hunter–gatherer camp when humans might look for and interact with potential mates.

Although this model measures the reproductive success of females, it does not explicitly include the introduction of new individuals into the population. Rather, the model runs in a steady state with the same number of adult individuals; offspring are merely counted towards female reproductive success.

See the Supplementary Information for the overview, design concepts, and details (ODD) protocol for this model, which contains the entire model schedule, parameters and additional information. The model can be downloaded from the Open Science Framework (OSF; <https://osf.io/c5pq7/>). The model was first programmed in NetLogo version 4.0.5 (ref. <sup>133</sup>) and then updated before publication to run on NetLogo version 6.1.1.

**Model schedule. Initial setup.** In total, 100 females and 100 males are created on the lattice, at a random location. This population size is based on estimated numbers for ancestral hunter–gatherer populations of between 100 and 250 (ref. <sup>136</sup>). Females are initiated with: (1) either a concealer or revealer strategy; (2) a random menstrual cycle day between 0 and 27; (3) a mate value, sampled from a Gaussian distribution ( $M=50$ ;  $s.d.=10$ ); (4) no current pregnancy; and (5) an aggressor or non-aggressor strategy, depending on the proportion of female aggressors in the population parameter (default = 100% except in experiment 1).

Females are also initiated with (6) fertile and infertile attractiveness multipliers, which determine their attractiveness at different stages of their menstrual cycle. For concealers, both fertile and infertile multipliers are set to 1, as they receive no increased attractiveness during ovulation. For revealers, the fertile multiplier is determined by a parameter (default = 1.25) and the infertile multiplier is either set to 1 (if revealers experience no reduction in attractiveness when not ovulating) or set such that the average attractiveness of revealers over one month is equal to that of concealers (default = 0.958).

Males are initiated with: (1) a mate value, sampled from a Gaussian distribution ( $M=50$ ;  $s.d.=5$ ); and (2) a promiscuity level of either 0 or 100, depending on a 'proportion of promiscuous males' parameter (default = 20%).

**Female procedures.** At each time step (representing one day), females first determine whether or not they are pregnant (Fig. 1). If they are not pregnant, they set their heading randomly, move forward by one patch and increment their menstrual cycle day by one. This is to simulate mate search. As with males (see below), it is assumed that females have a fundamental trade-off between offspring investment and mate search. If females are pregnant, they stay in the same patch and invest in their offspring by incrementing their offspring investment value by 1 each day. If offspring investment reaches 2,000, they increment their overall offspring count by 1, set their offspring investment value back to 0 and are no longer pregnant. The offspring investment value of 2,000 parent days of investment was chosen to approximate the human interbirth interval of three to four years<sup>137,138</sup>. If only the female is investing in the offspring, this would be equivalent to 2,000 days of uniparental investment (taking approximately 6 years, including pregnancy). If both the female and male are investing, this would be equivalent to 1,000 days of biparental investment (taking approximately 3 years, including pregnancy). Alternatively, these 2,000 units of parent days of investment can be reached by some combination of uniparental and biparental investment (which would fall between 1,000 and 2,000 days).

After females determine whether or not they are pregnant, all females set their current attractiveness value. Concealers set their current attractiveness value equal to their mate value, regardless of their menstrual cycle day, since their fertile and infertile attractiveness multipliers are both 1. Revealers, however, check their current menstrual cycle day: if the day is between 12 and 15, they are ovulating and so their current attractiveness is equal to the product of their mate value and their fertile multiplier. If the day is not between 12 and 15, they are not ovulating and so their current attractiveness is equal to the product of their mate value and their infertile multiplier.

Third, all females choose males to mate with. If there is at least one male on the current patch, females mate with the highest mate-value male. If their menstrual cycle day is between 12 and 15, females can get pregnant from this mating with a parameter-set probability (default = 30%), which then sets their menstrual cycle day to  $-1$ .

Finally, females can perpetrate aggression towards another rival female in the search radius (default = 2 patches), with a parameter-set probability (default = 100%). In experiment 2, females aggress towards the most attractive rival in this radius, but only if that rival is more attractive than they are. In experiment 3, females can target their aggression towards a randomly chosen female revealing ovulation within the search radius. Females with no rivals in their rival search radius do not aggress. The default cost to the female for perpetrating aggression is 0, although we varied this parameter in the results reported in the Supplementary Information. When females aggress against rivals, they do not keep a running list of every individual they have aggressed against; however, we tracked the acts of aggression and found that they were normally distributed (see Extended Data Figs. 7 and 8).

After aggression is perpetrated, the costs of aggression to rivals (cost to others) and to the aggressor (cost to self) are then added to an aggression damage variable (range 0–100). Aggression damage represents the damage to the target's attractiveness caused by aggression. The negative effects of past aggression are then reduced by proportion aggression damage decay (default = 0.01), to simulate recovery from reputational damage (see Supplementary Table 1). All females' current attractiveness values are then reduced by their current aggress damage proportion, and it is this current attractiveness value that is then visible to males engaged in mate search.

**Male procedures.** Males have a trade-off between investing in offspring or searching for mates; at each time step, they can only do one or the other (Fig. 1). The male promiscuity parameter determines this decision. If males are not promiscuous, they invest in the offspring of their current mate (that is, they increment their current mate's offspring investment value by 1). Each day (time step), if they do not have a mate, they move to the most attractive female in the search radius. If males are promiscuous, every time step, they set a random heading, move forward one patch, check in their mate search radius (default = 2 patches) for the most attractive female and move to her. If there are no females in the search radius, they set their heading randomly and move forward one patch.

**Model parameters.** Where possible, default model parameters were drawn from existing scholarship (Supplementary Table 1). Refer to Supplementary Table 3 for the model parameters used in all three main experiments.

**Simulations.** Simulations were run for 10,000 time steps, corresponding to 10,000 days or about 27.4 years. This was based on an approximate fertility window between the ages of 13 and 40 years in ancestral conditions<sup>139</sup>. The average lifetime reproductive success and paternal investment for each female strategy were measured at the end of each run. We ran simulations 10,000 times for all of the main experiments and 100 times per parameter value for all sensitivity analyses (note that this was more than we pre-registered, after a recommendation from an anonymous reviewer). We controlled for the initializing random seed in all model runs. All simulations were run using NetLogo version 6.1.1 (ref. <sup>135</sup>).

**Statistical analysis.** Data distributions were assumed to be normal upon inspection but this was not formally tested. Statistical analyses were conducted in R version 3.5.1 (ref. <sup>140</sup>) and the figures were produced with the ggplot2 package<sup>141–174</sup> (<https://osf.io/c5pq7/>). Paired two-tailed *t*-tests were used for all statistical comparisons, to account for the interdependency of both strategies within individual simulations. Data collection and analysis were not performed blind to the conditions of the experiments.

**Pre-registration.** This study was pre-registered on the OSF on 11 October 2017 (<https://osf.io/rq8z6/>).

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## Data availability

This study was pre-registered on the OSF. Open data and analysis code can be found in our OSF repository at <https://osf.io/c5pq7/>.

## Code availability

NetLogo models can be found in our OSF repository at <https://osf.io/c5pq7/>.

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## Author contributions

J.A.K., S.C., M.G.H. and A.A. developed and/or critically enhanced the underlying theorizing. J.A.K., M.R.F., M.C. and A.A. researched the underlying model parameters. A.A. wrote the initial model, which was subsequently modified by S.C. and M.C. S.C. and A.A. ran and reported the analyses. S.C. created all of the figures. J.A.K., S.C. and A.A. wrote and revised the manuscript with critical feedback from M.G.H. All authors approved the manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

**Extended data** is available for this paper at <https://doi.org/10.1038/s41562-020-01038-9>.

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41562-020-01038-9>.

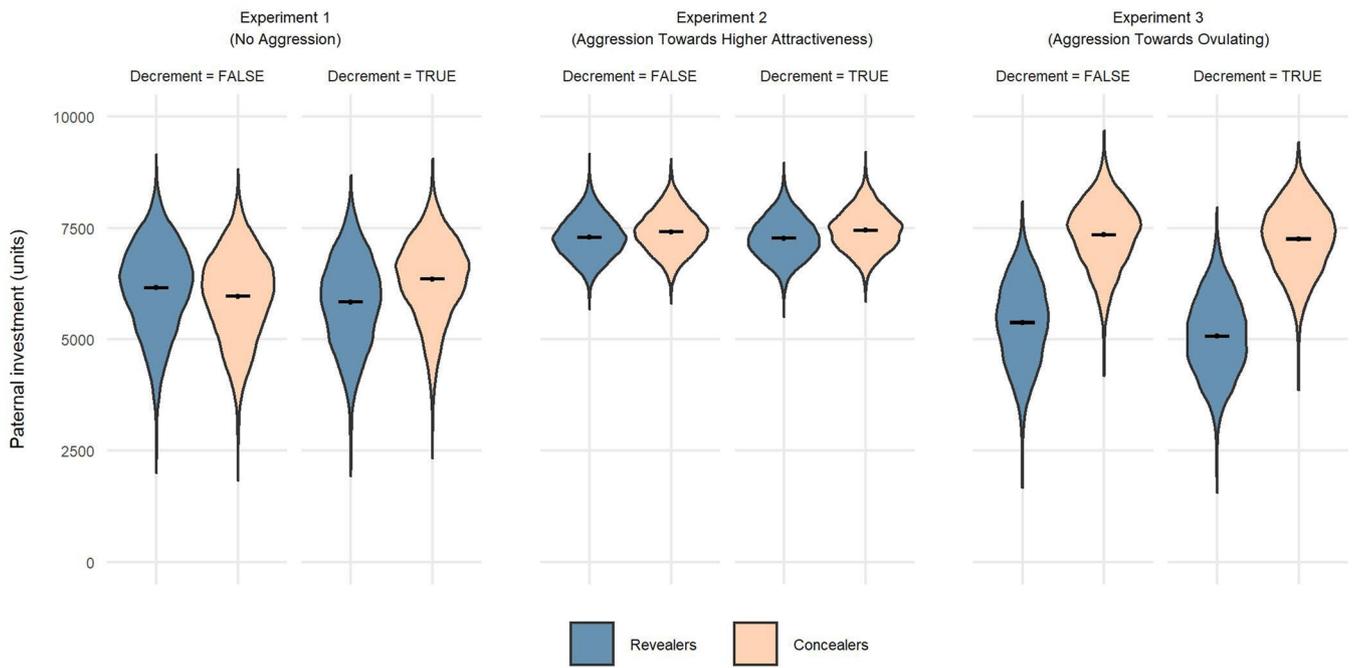
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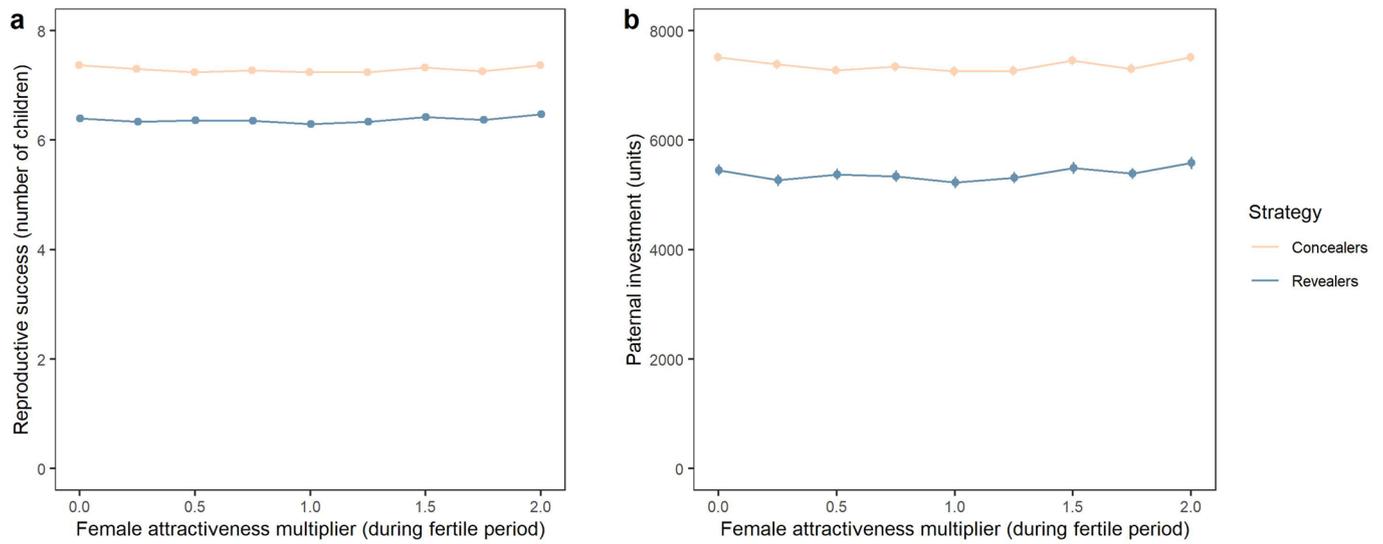
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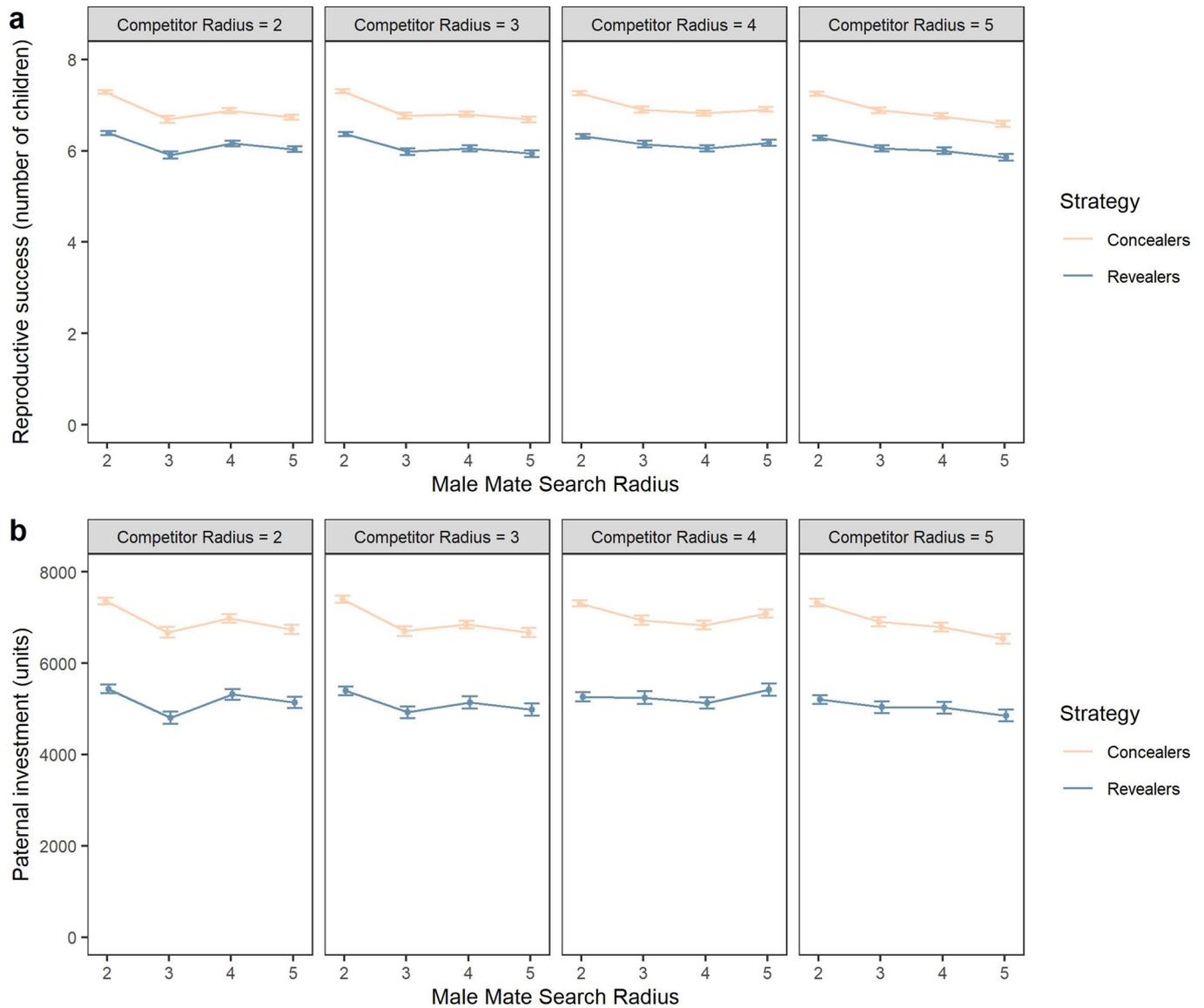
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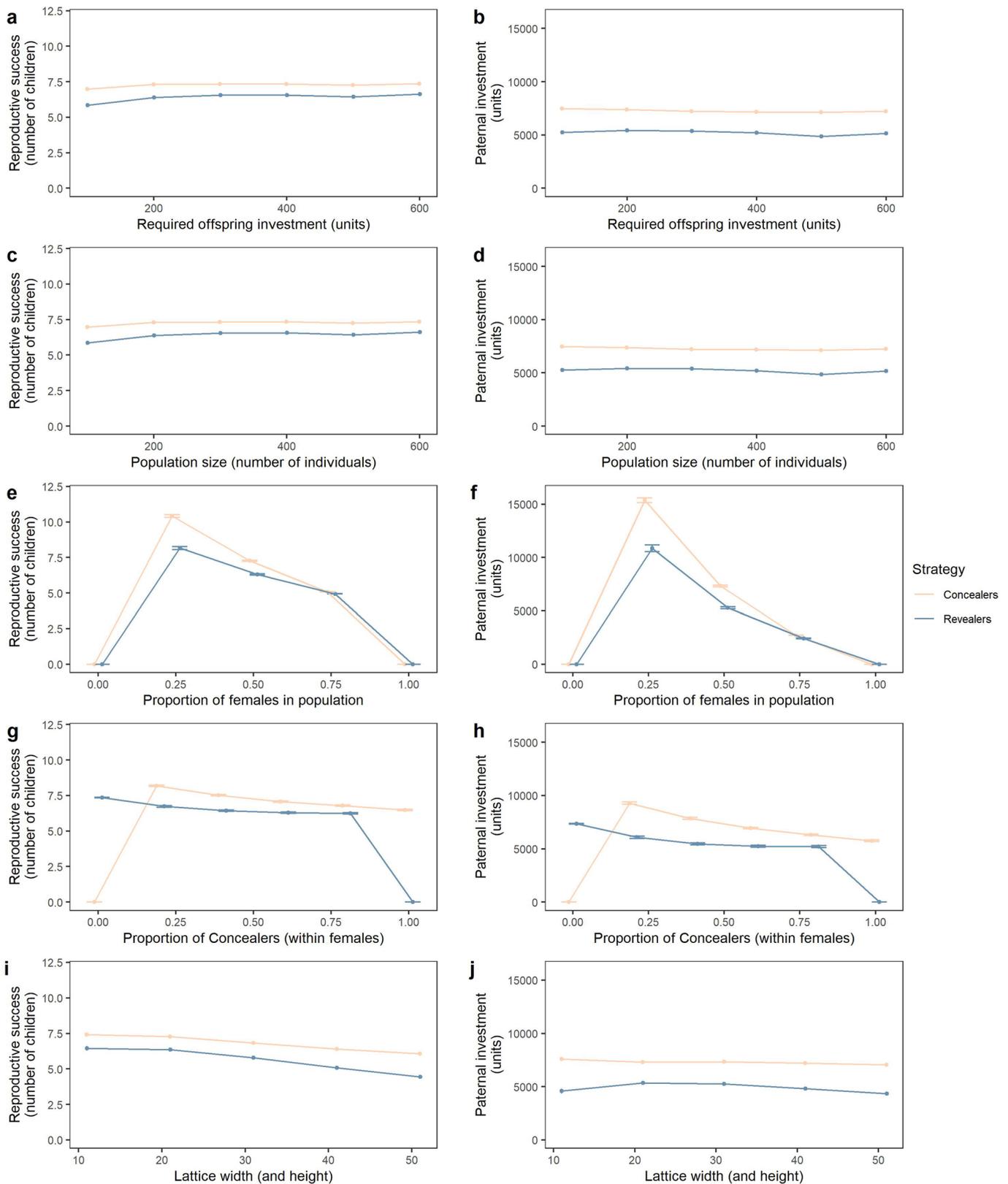
**Extended Data Fig. 1 | The paternal investment for Revealers and Concealers, after 10,000 time steps in the model.** Violin plots summarise the results of 10,000 independent model runs, bolded points are mean averages, and error bars are standard errors. Concealers consistently outcompete Revealers only in Experiment 3, under conditions of female aggression towards ovulating rivals. See Supplementary Table 5 for inferential statistics.



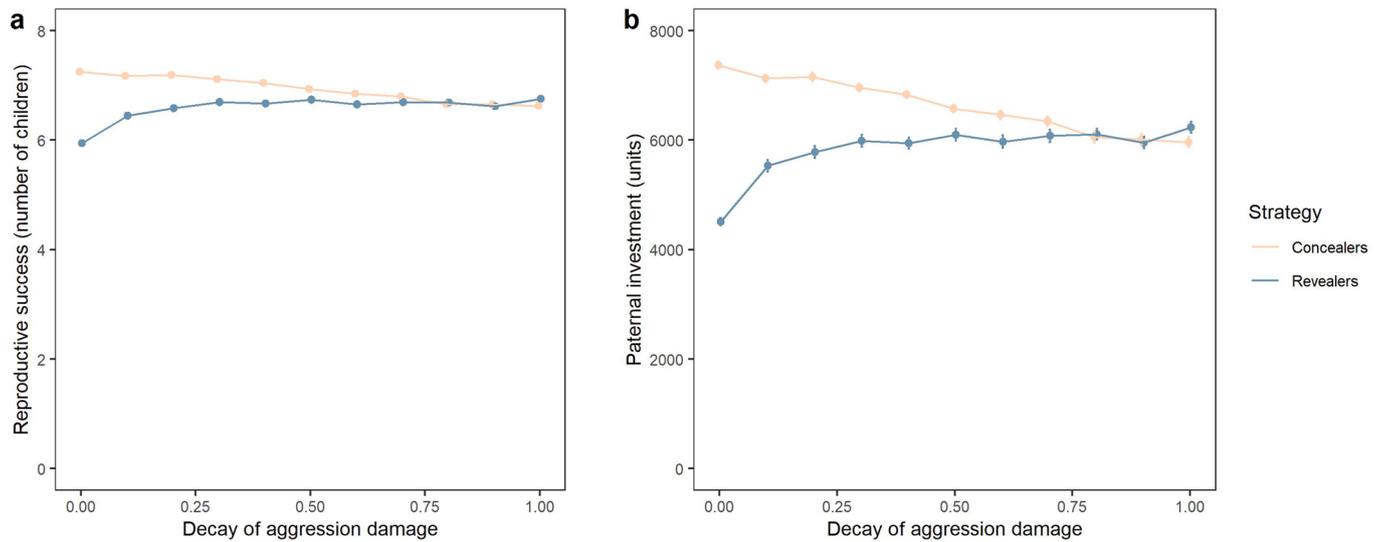
**Extended Data Fig. 2 | Varying the female attractiveness multiplier when fertile.** For both (a) reproductive success and (b) paternal investment, Concealers have an advantage over Revealers regardless of the fertility multiplier for Revealers. Points are mean averages across 100 independent model runs per parameter value, and error bars are standard errors. See Supplementary Table 6 for inferential statistics.



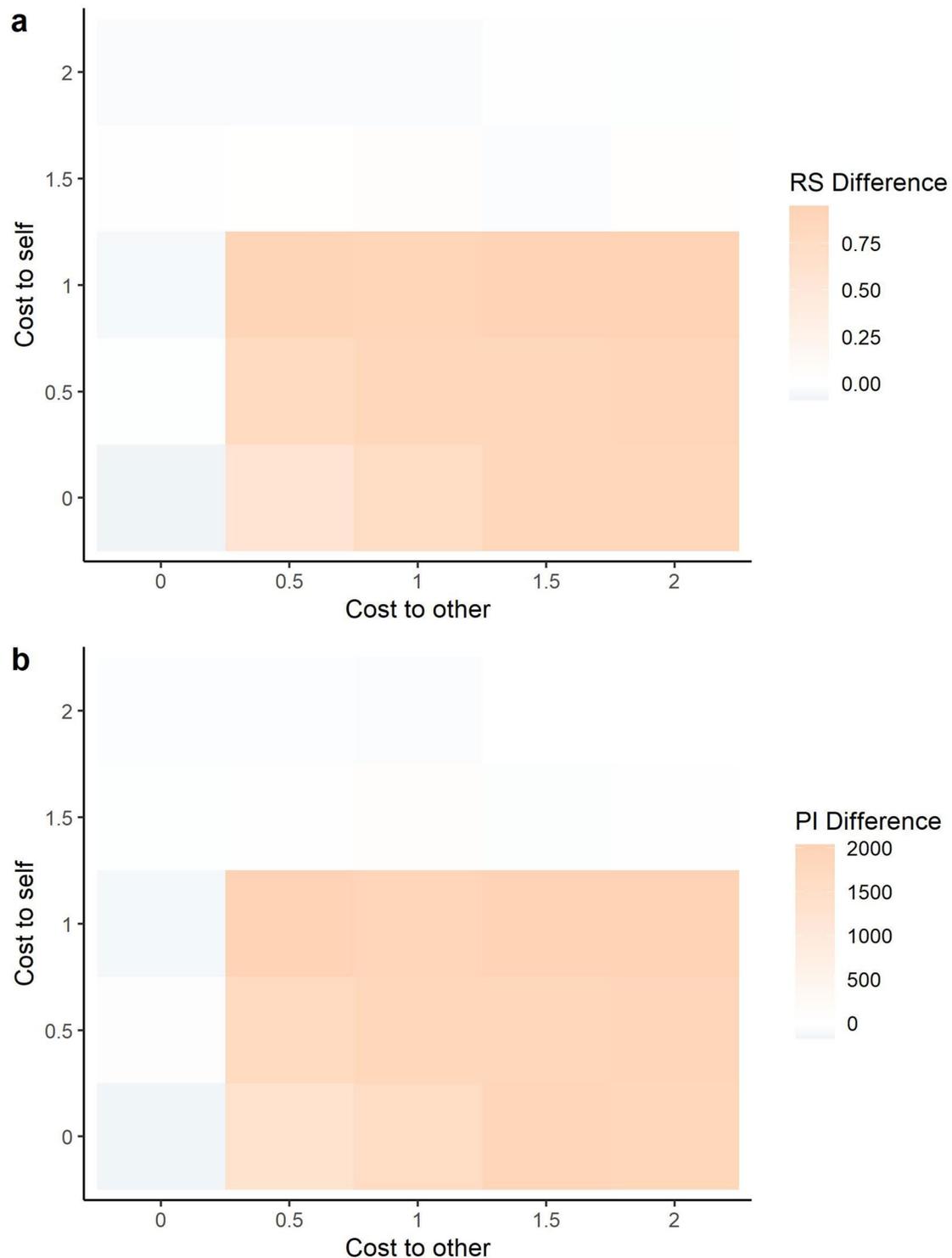
**Extended Data Fig. 3 | Varying the radius of competition (females) and mate search (males).** For both (a) reproductive success and (b) paternal investment, Concealers have an advantage over Revealers regardless of the radius of competition or mate search. Points are mean averages across 100 independent model runs per parameter value, and error bars are standard errors. See Supplementary Table 6 for inferential statistics.



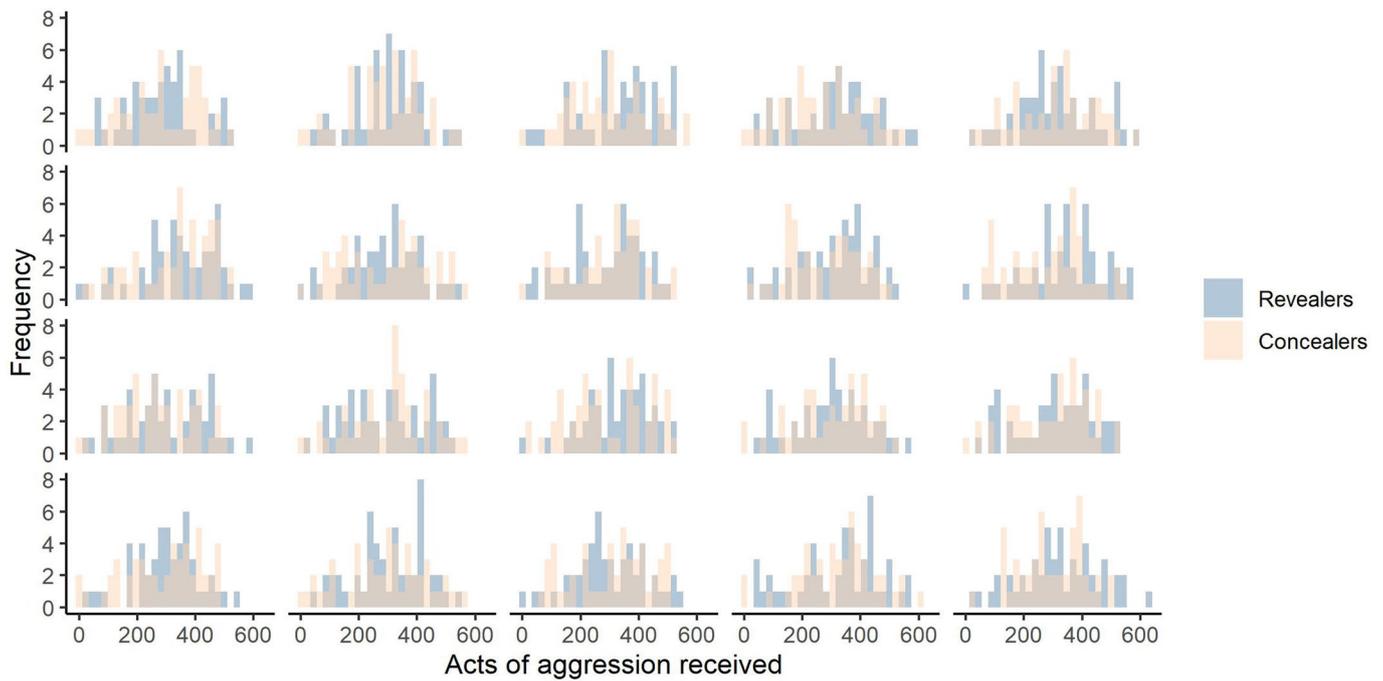
**Extended Data Fig. 4 | Further sensitivity analyses.** We vary the offspring investment amount (units) required to successfully have a child in the model, the number of individuals in the model (population size), the proportion of females in the population, the proportion of Concealers within the female population, and the size of the square world (lattice width is equal to lattice height). In all cases, Concealers have an advantage over Revealers. Points are mean averages across 100 independent model runs per parameter value, and error bars are standard errors. See Supplementary Table 6 for inferential statistics.



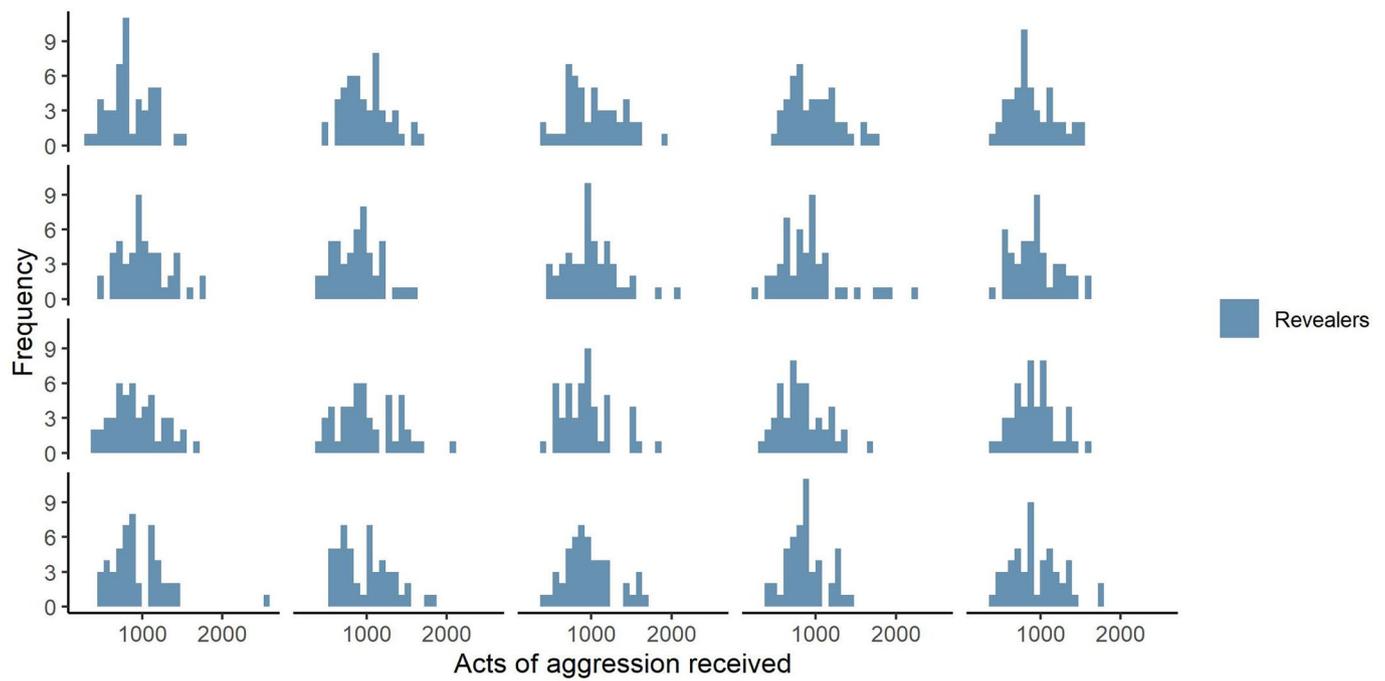
**Extended Data Fig. 5 | Varying the decay of aggression damage (that is, the speed at which females heal from aggression), where 0 means females never heal, and 1 means females heal immediately.** For both (a) reproductive success and (b) paternal investment, Concealers only have an advantage when the decay of aggression damage is less than or equal to around 0.6. Points are mean averages across 100 independent model runs per parameter value, and error bars are standard errors. See Supplementary Table 6 for inferential statistics.



**Extended Data Fig. 6 | Tile plots summarizing the Concealer advantage with varying costs of aggression, to both self and other (target).** As tiles become increasingly beige, Concealers have more of an advantage (that is, positive raw difference in either number of children or paternal investment units). For both **(a)** reproductive success and **(b)** paternal investment, Concealers only have an advantage when the cost to self is low ( $< 1$ ), and the cost to other is positive ( $> 0$ ). Values are averaged over 100 independent model runs per parameter value. See Supplementary Table 6 for inferential statistics.



**Extended Data Fig. 7 |** The number of aggression acts Concealers and Revealers received after 10,000 time steps in the model, across 20 different model runs all with the default parameters for Experiment 2, where females aggressed towards the most attractive female nearby females (not necessarily the ovulating females). Concealers received 294 acts of aggression on average ( $SD = 131$ ). Revealers received 308 acts of aggression on average ( $SD = 127$ ), significantly more than Concealers (GLMM;  $p = 0.01$ ). Aggression amounts appear normally distributed, with few outliers.



**Extended Data Fig. 8 |** The number of aggression acts each Revealer received after 10,000 time steps in the model, across 20 different model runs all with the default parameters for Experiment 3, where females aggressed towards the nearby ovulating females. Concealers were never the targets of aggression. Revealers received 941 acts of aggression on average ( $SD = 312$ ). Aggression amounts appear normally distributed, with few outliers.

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Research sample	The research sample consists of agents from our simulations (default 100 male and 100 female) per simulation. We ran simulations 10,000 times for all main experiments, and 100 times per parameter value for all sensitivity analyses
Sampling strategy	We averaged over all Revealer and Concealer strategies at the end of each model run. No formal sample-size calculation was performed, but we increased the number of runs for main simulations from 100 to 10,000 based on a recommendation from an anonymous reviewer.
Data collection	NetLogo Version 6.1.1 was used to run the simulations and collect data. Data collection and analysis were not performed blind to the conditions of the experiments.
Timing	Data collection using NetLogo Version 6.1.1. was conducted in October 2019.
Data exclusions	No data were excluded from analyses
Non-participation	There were no dropouts.
Randomization	Agents were randomly given Concealer or Revealer strategies upon initialisation of each model simulation.

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