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The role of familiarity in signaller–receiver interactions

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In animal communication, individuals of species exhibiting individual recognition of conspecifics with whom they have repeated interactions, receive signals not only from unfamiliar conspecifics, but also from individuals with whom they have prior experience. Empirical evidence suggests that familiarity with a specific signaller aids receivers in interpreting that signaller's signals, but there has been little theoretical work on this effect. Here, we develop a Bayesian decision-making model and apply it to the well-studied systems of primate ovulation signals. We compare the siring probability of learner males versus non-learner males, based on variation in their assessment of the best time to mate and mate-guard females. We compare males of different dominance ranks, and vary the number of females, and their cycle synchrony. We find strong fitness advantages for learners, which manifest very quickly. Receivers do not have to see the full range of a signaller's signals in order to start gaining familiarity benefits. Reproductive asynchrony and increasing the number of females both enhance learning advantages. We provide theoretical evidence for a strong advantage to specific learning of a signaller's range of signals in signalling systems. Our results have broad implications, not only for understanding communication, but in elucidating additional fitness benefits to group-living, the evolution of individual recognition, and other characteristics of animal behavioural biology.

1. Introduction

In animal communication, individuals often receive signals not only from unfamiliar conspecifics, but also from conspecifics with whom they have prior experience. Many species seem to navigate such interactions by developing individual recognition, which can occur in multiple contexts [1,2]. These include recognition of nearby rivals and neighbouring territory holders (e.g. birds [3], lizards [4,5], anurans [6], fish [7,8], crustaceans [9]), recognition between parents and offspring (e.g. penguins [10,11], songbirds [12], ungulates [13,14], bats [15–17], pinnipeds [18–20], dolphins [21]), and recognition within individuals in dominance hierarchies in social groups (e.g. insects [22,23], crustaceans [24,25], fish [26,27], ungulates [28], carnivores [29,30], primates [31]). Repeated interactions with individuals that can be individually recognized may be important in allowing receivers to learn about the behaviour of specific signallers [32]. Such contexts also allow receivers to attend more to specific signallers that have demonstrated signal reliability, and provide a mechanism that can ensure signal honesty [33]. Such effects have been studied in relation to alarm calls, where theoretical models demonstrate fitness benefits that accrue to individuals discriminating between specific signallers [34], and where empirical data suggests that receivers do indeed preferentially attend to the calls of reliable signallers (e.g. vervet monkeys [35]; marmots [36]).

Individual recognition between signallers and receivers may be also be important not for assessing whether a signaller is reliable or unreliable, but for determining whether a conspecific's signal expression value is relatively low or high, which may depend on the range of signals that each specific signaller expresses. Empirical data on the female fertility signals of humans and other primates have indeed shown that familiarity with a specific signaller can aid a receiver in interpreting that signaller's signals or cues. For example, heterosexual men seem better able to assess the timing of their partner's fertile periods relative to strangers, simply by apparent cues from sight or smell [37–39]. In baboons, males who have spent longer in a social group consort with females during conceptive cycles more frequently compared to males who are new arrivals [40], while long-tailed macaques from the same social group as a specific female are better at timing their mating effort to the fertile periods of that female compared to other males [41]. Experiments have also shown that male rhesus macaques that are familiar with females are more likely to look longer at images of the ovulatory faces of those females compared to other males [42]. However, despite such empirical evidence, to our knowledge there has been no theoretical work of any type undertaken to address the role of signaller–receiver familiarity on the efficacy of signal interpretation by receivers.

Here, we develop a Bayesian decision model to ask how experience with a signaller affects the efficacy of a receiver in interpreting that signaller's signals and behaving optimally in response. As a case study, we take the intra-cycle fertility signals exhibited by many anthropoid primate species. Examples of these signals include the sexual swellings of species such as baboons and chimpanzees, the facial colour changes of species such as Japanese and rhesus macaques, and the chest-patch colour changes of geladas [43]. In all cases, signal expression is low when the female is not fertile, and then increases steadily until a maximal expression period, during which ovulation occurs [44]. However, different females have very different minima and maxima. Simple rules such as 'choose the female with the largest swelling' appear to be suboptimal, as some females exhibit swellings that when maximal around ovulation are still smaller than those of other females not currently ovulating (e.g. [45]). The advantages of formalizing the model for this paradigm include that: (i) primate intra-cycle fertility signals have been well-studied empirically, such that we have a good understanding of the mechanisms of cyclical changes in females, the nature of behavioural responses in males, and the observed inter-female differences in both swellings and male behavioural interest; (ii) several studies have suggested that males familiar with specific females may perform better in assessing whether that female is fertile based on her signal [42], and may also time their mating effort more accurately with such females [40,41].

Our model is developed from a long tradition of Bayesian models of perception (for reviews, see [46–48]). In such models, the observer computes a posterior probability distribution over the world state variable of interest given noisy sensory measurements. Computing the posterior requires that the observer has internalized knowledge of the statistics of the environment, as well as of the process generating the measurements. If such knowledge is matched to the true statistics, like we assume here, the Bayesian model is also referred to as an optimal-observer or ideal-observer model. Our model is based on five males of different dominance ranks making mating decisions between a number of cycling females with different levels of signal expression. We vary the number of females (5, 10, 15) and the synchronicity of their cycles (low versus high synchrony), to investigate the effects of changing key biological parameters that have been demonstrated to affect the function of these types of signals. Our overall aim is to provide theoretical assessment of the potential advantages of receiver familiarity on signal interpretation, to explore how such advantages manifest, and to assess how they are affected by biologically realistic changes to the contexts in which receivers observe such signals.

2. Methods

The models consist of two stages: a measurement model, also called a generative model, which specifies the probability distribution of the male's measurements as a function of time for different females, and a male decision model, in which the male either does or does not learn. Learning is implemented as Bayesian: the learner updates a posterior distribution from day to day based on the measurements as well as knowledge of the measurement model. Learning does not necessarily require recollection, recognition or higher-order cognition.

2.1. Measurement model

We construct a statistical model of visual measurements of a sexual swelling or a facial colour change during a female's menstrual cycle, where the parameters of that cycle are heterogeneous across females. We define time as 30 discrete days, which is a fairly typical cycle length for an anthropoid primate [43]. We assume that the measured signal, denoted by x_t for day t, follows a sinusoidal function corrupted by zero-mean Gaussian noise:

$$x_t \sim \text{normal}(\bar{s} + A\cos(\omega(t-\tau)), \sigma^2),$$

where $\bar{s}$ is the cycle-averaged signal size or lightness, A the amplitude of signal variation, τ the ovulation time, $\omega = 2\pi/(30\text{ days})$ the frequency of the cycle, and σ the standard deviation of the noise. If A is positive, then the signal is on average maximal at ovulation. We assume that the noise is uncorrelated across time points. We allow the parameters $\bar{s}$, A and τ to differ across females. To model such variation, we assume that the signal average $\bar{s}$ is independently drawn for each female, from a normal distribution with mean $\mu_{\bar{s}}$ and variance $\sigma_{\bar{s}}^2$:

$$\bar{s} \sim \text{normal}(\mu_{\bar{s}}, \sigma_{\bar{s}}^2).$$

Similarly, we assume that signal amplitude A is independently drawn for each female from a normal distribution with mean μ_A and variance σ_A^2:

$$A \sim N(\mu_A, \sigma_A^2).$$

This yields a total of five parameters: σ, $\mu_{\bar{s}}$, $\sigma_{\bar{s}}$, μ_A and σ_A. Since the problem is invariant to shifting and scaling, we can fix two parameters; we use this freedom to set $\mu_{\bar{s}} = 0$ and $\sigma_{\bar{s}} = 1$. We choose the remaining three parameters to produce a plausible set of cycles (figure 1*a*): $\mu_A = 1$, $\sigma_A = 0.33$ and $\sigma = 0.33$. Changing these parameters will not qualitatively change our results. However, there will be quantitative differences. In particular, we expect the benefits of learning to be greater when σ_A is higher.

We vary the degree of reproductive synchrony in the measurement model. Reproductive synchrony—the overlap of females' fertile phases—is considered to be one of the single most important parameters affecting the evolution of these signals, as well as male responses [44]. This is because when females are highly asynchronous, high-ranking males can monopolize all female fertile phases, but when females are highly synchronous, reproduction is inevitably shared between multiple males. We simulate two synchrony conditions: low synchrony—ovulation time τ is drawn from a uniform distribution over the cycle; high synchrony—ovulation time is drawn from a Gaussian distribution with mean at Day 15 and standard deviation 3. In both conditions, the ovulation times of different females are uncorrelated.

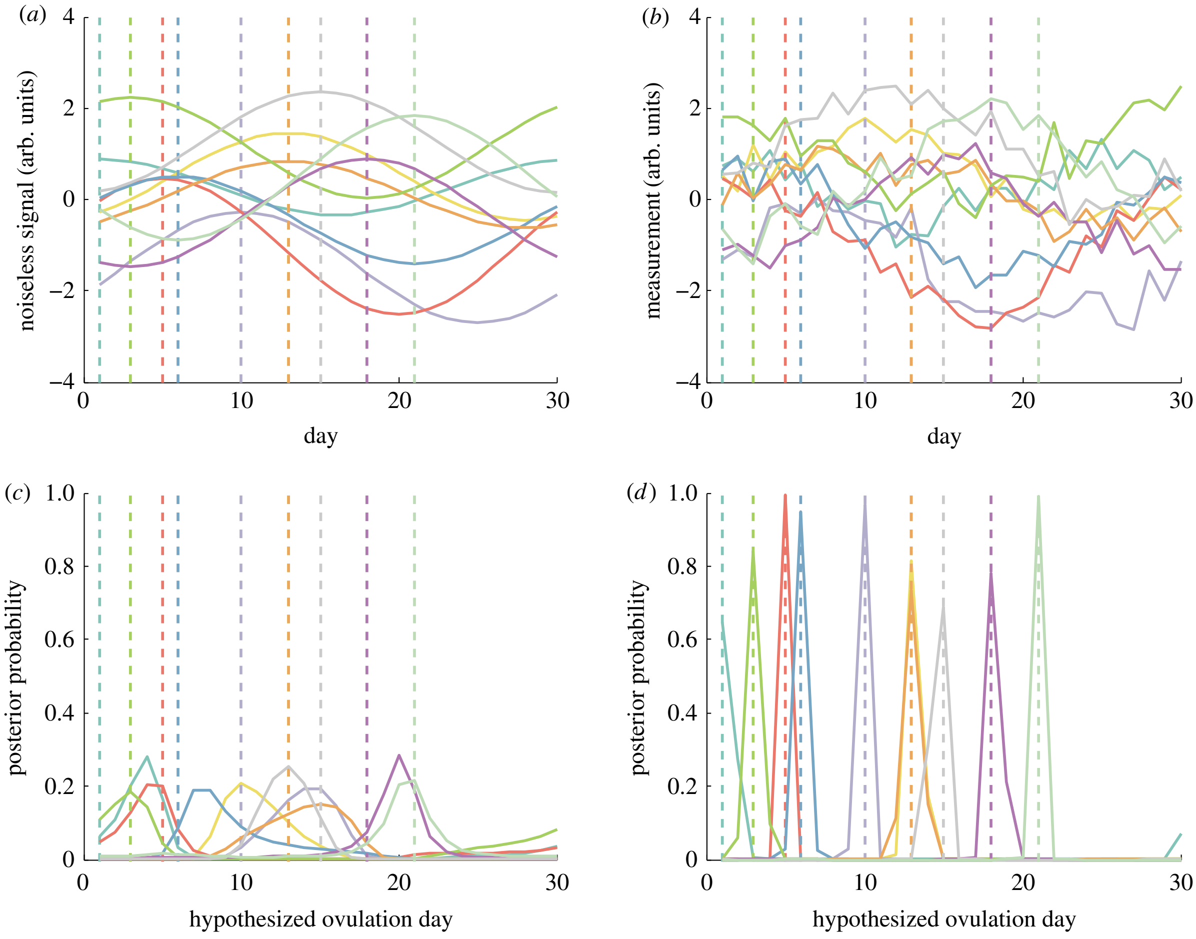

Figure 1. Cyclical variation in female signal expression (*a*), male measurements of those cycles (*b*), posteriors after 10 (*c*), and 30 (*d*) days.

2.2. Decision models

After observing a given female for T days, a male has a set of measurements $x_1, x_2, \ldots, x_T$. We assume that each male mates with only one partner a day and a female mates with at most one partner a day, reflecting consortship and/or male mate guarding [43]. We further assume that a female is receptive to a male if no higher-ranked male is consorting with her on that day. We consider a non-learning and a Bayesian learning decision model.

2.2.1. Non-learner

We model the non-learner as following the heuristic rule of always mating with the available female with the highest level of signal expression, i.e. the female with the highest x_T.

2.2.2. Learner

By contrast, the Bayesian learner computes for each female a posterior distribution over ovulation time, $p(\tau|x_1, x_2, \ldots, x_T)$. We assume that in computing the posterior, the male assumes that the distribution of ovulation time in the population, $p(\tau)$, is uniform. This assumed distribution is matched to the true distribution in the low-synchrony condition but mismatched in the high-synchrony condition. Therefore, the learner could gain an additional advantage in that condition by using knowledge of the true distribution (see Discussion). The posterior distribution is derived in the electronic supplementary material and examples are shown in figure 1. Posteriors become narrower over time.

Finally, the Bayesian learner model assumes that the male mates with the available female who has the highest probability of being fertile. Being fertile means that ovulation time τ falls within the next L days (including the current day), $\tau \in \{t, \ldots, t+L-1\}$. The probability that the female is fertile is thus the posterior probability over τ summed over the current day and the following $L-1$ days:

$$p_{\text{fertile}}(t) = \sum_{\tau=t}^{t+L-1} p(\tau|\mathbf{x}). \tag{2.1}$$

2.3. Siring probability

We have defined the decision strategies of a non-learning and of a learning male. To assess the effectiveness of either strategy, we have to connect mating success to reproductive success (the siring of offspring). For a given female, a male's probability of siring is 0 if he does not mate with her during her fertile period, but what is it otherwise? Sperm longevity is limited, but here we assume that it extends to at least the duration of the fertile period (4 days) [49]. However, sperm of multiple males who mate with the same female during her fertile period will be subject to sperm competition [43]. To reflect this, we make the simplifying assumption that when the same female mates k times within her fertile period, the probability of any mating leading to siring is

$$p(\text{siring}|k, \text{fertile}) = \frac{1}{k}. \tag{2.2}$$

We assume a 4 day fertile period (e.g. [49]), so that on a given day, the siring probability for a given male with any given female can take the values 0, 1/4, 1/3, 1/2 and 1. If the same male mates with the same female on more than 1 day during the fertile period, the male will receive a siring probability of $1/k$ for every day mating. However, the assumption does not capture the possibility that sperm viability decreases over the duration of the fertile period, or the possibility that later males remove the sperm of earlier males; both factors will in reality confer a disadvantage to a male who mates with the female earlier in her fertile period.

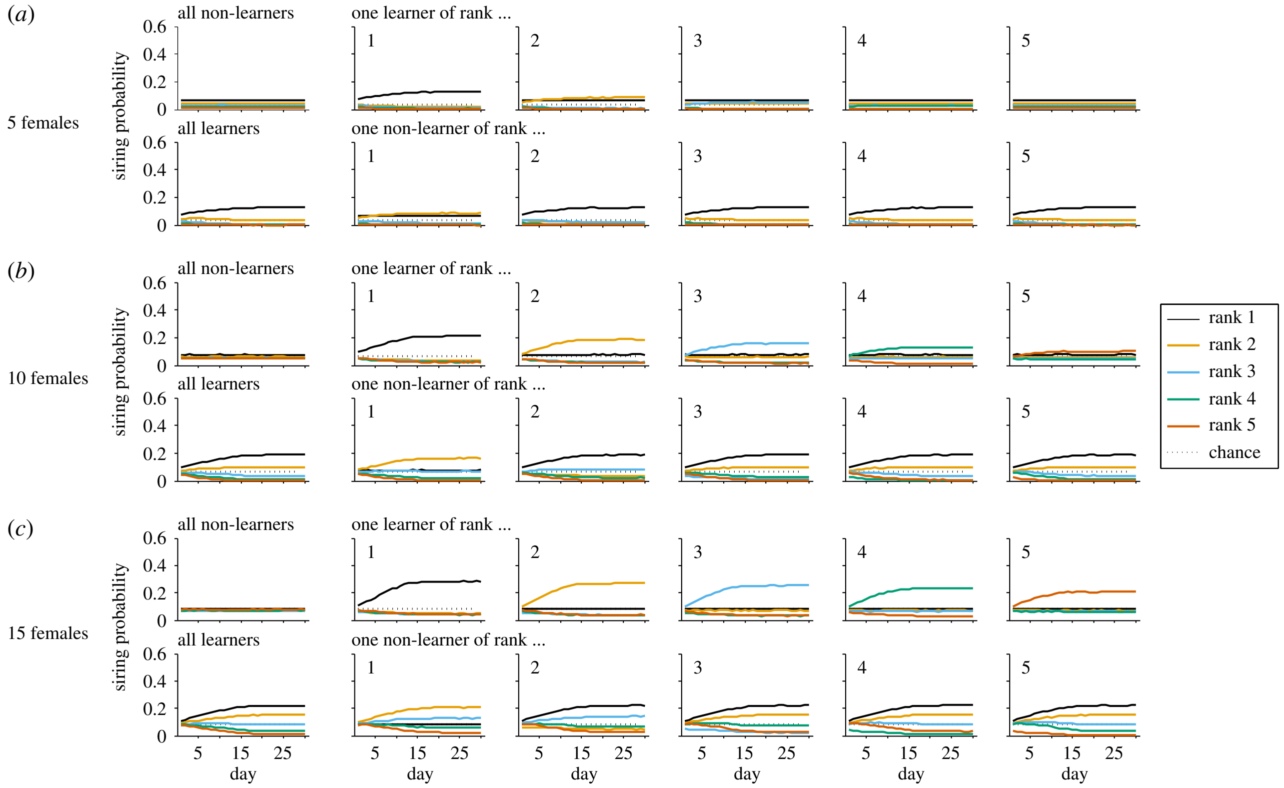

Figure 2. Siring probability in the low-synchrony condition with 5 (*a*), 10 (*b*), and 15 (*c*) females. In each of the subplots (*a*–*c*), the top left panel represents a population of all non-learners; the other panels in the top row represent populations with one learner (of varying rank, indicated by the number inside each panel) among non-learners; the bottom left panel represents a population of all learners; and the other panels in the bottom row represent populations with one learner (of varying rank) among non-learners. Each panel shows the siring probabilities of all five males in the same population. The dotted line corresponds to chance—the siring probability in a population in which all males randomly choose a female to mate with.

2.4. Simulations

We assess the non-learner and learner strategies by calculating through simulations the expected probabilities of siring offspring under these strategies. We simulate groups consisting of five males and five, 10, or 15 females. We consider 12 male learning conditions: (i) all males are non-learners; (ii) all males are learners; (iii) one male is a learner (in each of five possible ranks), and all others non-learners; (iv) one male is a non-learner (in each of five possible ranks), and all others learners. The highest ranking male makes the first choice, followed by each male sequentially in order of dominance. We factorially combine all conditions, for a total of 2 (synchrony) × 3 (numbers of females) × 12 (learning conditions) = 72 conditions.

The sharing of the siring probability over the fertile period introduces boundary effects. For example, if on the first day in the simulation, a male mates with a female with $\tau = 1$, then he will be guaranteed a siring probability of 1, since there is no need to share with males who mated with her on the preceding days. Similarly, if a male mates on the last day of the simulation with a female who ovulates 3 days later, he will not have to share either. This artificially inflates the siring probabilities on the ends. To avoid these boundary effects, we simulate 36 days instead of 30 days, but only report performance in the central 30 days; in other words, we pad the simulated time period on both ends by a number of days equal to the length of the fertile period minus 1.

In each of the 72 conditions, we perform 10 000 simulations (based on precedent, and the number of simulations typically required to ensure convergence in such studies). In each simulation, we draw new cycle parameters $\bar{s}$ and A for each female, and a new set of noisy measurements x, one for each female and each day. Then, on each day, we evaluate the decision rules of the males in descending rank order. This gives a matrix of IDs of chosen females as a function of day and male. We score this choice matrix against the true ovulation times, giving a matrix of siring probabilities. Finally, we average this matrix across all simulations and restrict ourselves to the central 30 days. We plot the values in these siring probability matrices by condition, giving rise to the 72 plots in figures 2–4.

2.5. Calculation of chance

We define chance as the siring probability in a population in which every male randomly chooses a female to mate with. This probability is equal to the product of the probability that the female is fertile and the siring probability given that she is fertile:

$$\text{chance}(t) = p_{\text{fertile}}(t) \cdot p(\text{siring}|\,\text{fertile}). \qquad (2.3)$$

The first factor in equation (2.3) takes a form similar to equation (2.1) but uses the actual ovulation time distribution rather than a posterior:

$$p_{\text{fertile}}(t) = \sum_{\tau=t}^{t+L-1} p(\tau).$$

In the low-synchrony condition, $p_{\text{fertile}}(t)$ is equal to $L/30$. In the high-synchrony condition, it is easily computed numerically. The second factor in equation (2.3) needs to be broken down by the number of times the female mates during her fertile period; we denote this number by k. Then,

$$p(\text{siring}|\,\text{fertile}) = \sum_{k=1}^{L} p(k)p(\text{siring}|k;\ \text{fertile}). \qquad (2.4)$$

Here, $p(\text{siring}\,|\,k, \text{fertile})$ is given by equation (2.2), and $p(k)$ is the probability that the female mates exactly $k-1$ times in the $L-1$ days of the fertile period excluding the current day. The probability of mating on a given day is $n_{\text{males}}/n_{\text{females}}$, and therefore $p(k)$ is the probability of $k-1$ 'successes' among $L-1$

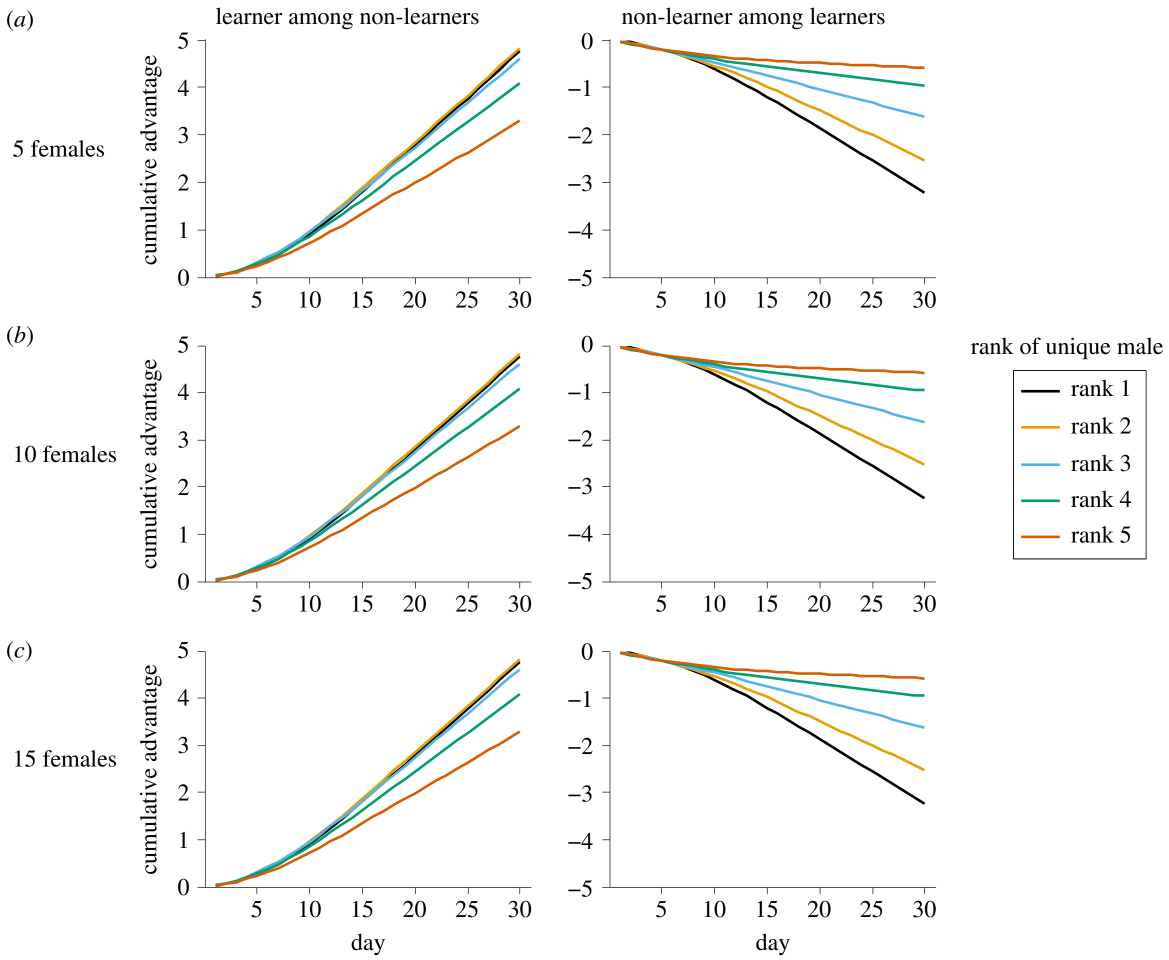

Figure 3. Cumulative advantage in siring probability in the low-synchrony condition with 5 (*a*), 10 (*b*), 15 (*c*) females. Left column: one learner among non-learners, with each colour corresponding to a different rank of the learner. Right column: one non-learner among learners, with each colour corresponding to a different rank of the learner. Unlike in figure 2, each colour within the same panel represents a different population.

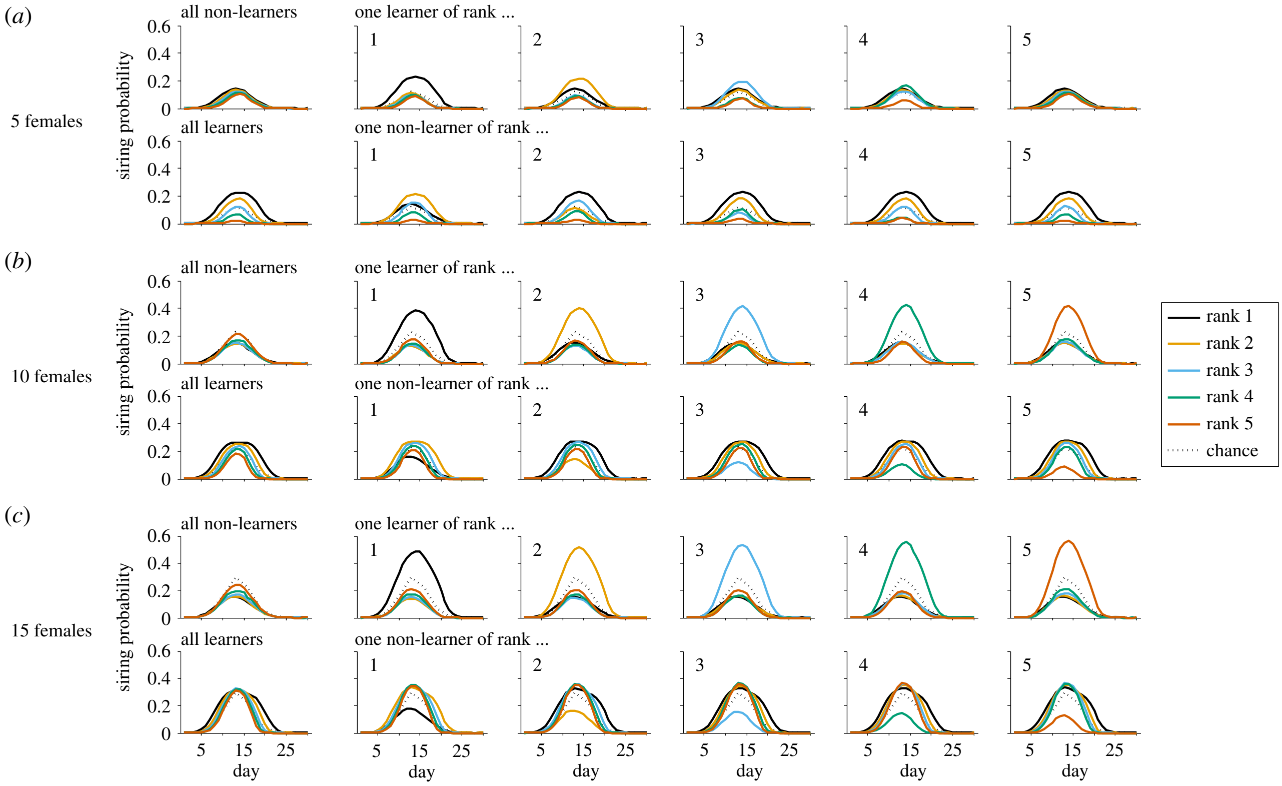

Figure 4. As figure 2, but for the high-synchrony condition.

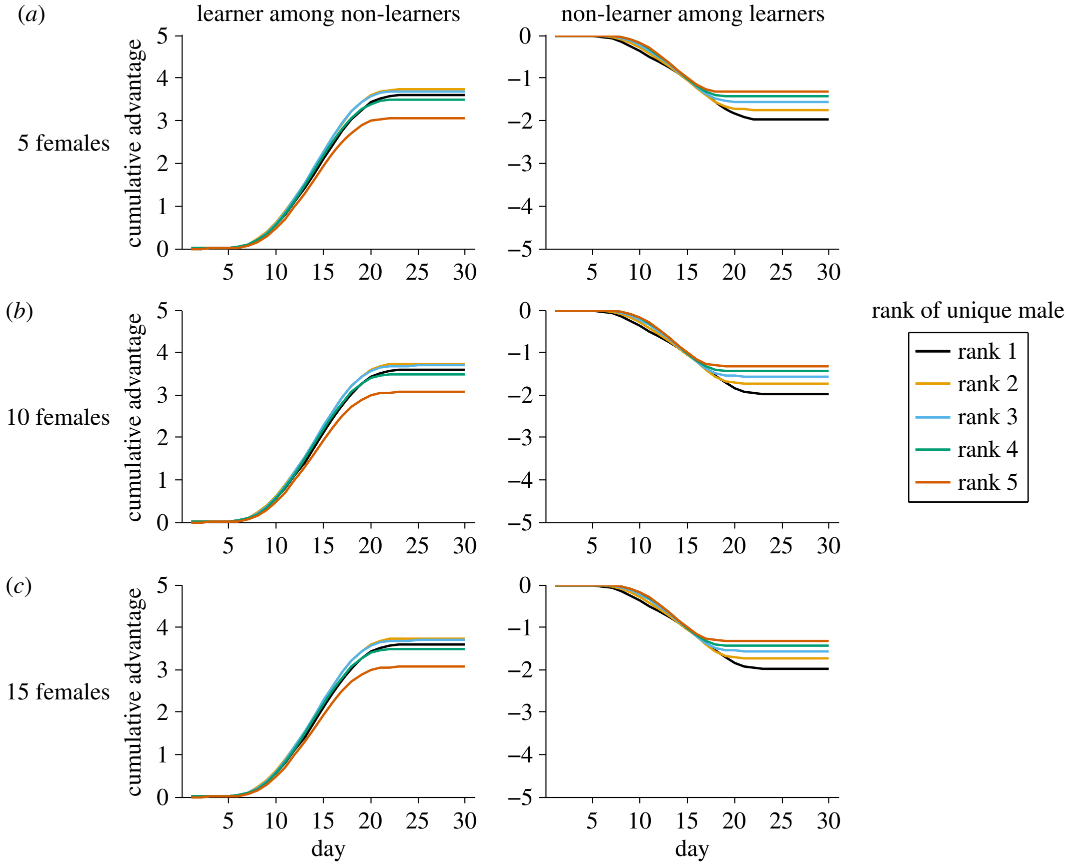

Figure 5. As figure 3, but for the high-synchrony condition.

Bernoulli trials with parameter $n_{\text{males}}/n_{\text{females}}$, which is given by the binomial distribution:

$$p(k) = \text{binomial}\left(k-1;\ L-1,\ \frac{n_{\text{males}}}{n_{\text{females}}}\right). \tag{2.5}$$

Combining equations (2.2) through (2.5), we find

$$\text{chance}(t) = \left(\sum_{\tau=t}^{t+L-1} p(\tau)\right) \times \left(\sum_{k=1}^{L} \frac{1}{k} \cdot \text{binomial}\left(k-1;\ L-1,\ \frac{n_{\text{males}}}{n_{\text{females}}}\right)\right).$$

Chance is plotted as a function of time in figures 2 and 4.

2.6. Code sharing

All code is available from the Dryad Digital Repository at: http://dx.doi.org/10.5061/dryad.t0680db [50].

3. Results

Under both low- and high-synchrony conditions, male learners have very marked advantages over non-learners.

3.1. Low synchrony

Under conditions of low female cycle synchrony, males that are learners among non-learners very quickly accrue sustained reproductive benefits (figure 2), representing a significant fitness advantage (figure 3). In contrast, being a non-learner among learners produces a serious reproductive and fitness disadvantage. Effects begin to accrue extremely quickly (within several days rather than several weeks), and do not require a sustained period of observation to emerge. Since female cycles are asynchronous, increasing the number of females increases the extent of the effect—learner males exposed to a larger number of females simply mate with a larger number of fertile females (figures 2 and 3). This cumulative benefit continues to rise over time as more and more females can be mated with.

3.2. High synchrony

Under conditions of high female cycle synchrony, males that are learners among non-learners also quickly accrue sustained reproductive benefits (figure 4), again representing a significant fitness advantage (figure 5). Since female cycles are synchronous, the cumulative benefit plateaus, and does not continue to increase beyond a threshold, with that threshold set by the total number of available female (figure 5).

4. Discussion

In this study, we modelled an intriguing phenomenon that has been empirically demonstrated, but which has had no theoretical basis on which to estimate the nature, strength and manifestation of its effects. Specifically, receivers often respond to signals given by familiar signallers, and place the signal within the context of the range of signals usually exhibited by that signaller. In modelling this phenomenon, we found a number of important general results, some of which were unexpected. Important and general conclusions include that the effect of learning the range of signals given by a specific signaller are very marked, and that they manifest extremely quickly. The latter result is particularly interesting. Since in our scenario there is a general function underlying female changes in signal expression, males are quickly able to estimate each female's specific function parameters to estimate her relative maximum expression without observing the whole function. This suggests that in at least some biological contexts, receivers do not have to see the full range of a signaller's signals in order to start gaining familiarity benefits. Observation by a receiver of just a subset of a signaller's signal variation may be enough to begin estimating the full range of that signaller's expected signal variation. Improved ability to learn is in this case selected for because males who learn will have higher reproductive success over time, favouring the spread of the strategy through the population. Male learning is not however reinforced by feedback during the lifespan, which might be seen in other contexts (for example, when predators learn about camouflaged prey, [51]). In this scenario, males learn by observing the rate of change in signal size, because there is an evolved underlying structure to signal change (cyclical), which only needs parameters to be estimated in order to be able to estimate aspects of the curve such as peaks and troughs.

Our modelled scenario is most directly relevant to a number of primate systems in which cyclical signals of fertility are exhibited. This includes species exhibiting sexual swellings such as chimpanzees, baboons, and many species of macaques, but also species that do not exhibit sexual swellings, but do exhibit coloration changes in the face (e.g. rhesus macaques), or other areas (e.g. the chest, gelada) [43]. Such signals are generally known to be probabilistic in nature, with signal expression high when the probability of conception is high, and low when it is low [44]. They are generally thought to evolve as mechanisms for indirect female mate choice, when direct female mate choice is limited, perhaps by marked sexual dimorphism, and male coercion. This suggests that *direct* female mate choice may not be predicted to have a large effect on our model.

One interesting question is how selection is likely to be acting on signallers versus receivers in this scenario. If females are selected to display a probabilistic signal as a mechanism of indirect mate choice, selection might then act on male receivers to improve their ability to learn, and hence their ability to obtain information from such a signal. In addition, females might be selected for signals that favour familiar males, in order to encourage males to remain in groups for longer periods, and/or to spend more time in association with specific females. This is predicted where females receive direct benefits from males, such as protection of infants from predators, and tolerance at food patches from which they might normally be excluded [44]. Selection may also act on males to improve their abilities at individual recognition more broadly, and on females to exhibit signals that enable individual recognition.

In addition to cyclical signals of female fertility, there are also other scenarios where the integration of social knowledge about specific individuals with information obtained by their signals seems likely to be important. These include in dominance interactions in group-living species where dominance hierarchies are formed, and where high dominance rank is accompanied by signals of high social status. In primates this includes signals in polygynandrous species (e.g. visual signals, mandrills, [52]; drills [53]; vocal signals, crested macaques, [54]) or in species that exhibit one-male units (e.g. visual signals, gelada [55]).

Although the model was developed for a cyclical signal, this general benefit should be applicable to other signal types, since the underlying decision problem—estimating parameters that describe the range of signals that a specific signaller gives—is a very common element of receiver decision-making across many types of signal. The general benefits to receivers of learning the signal range of specific signallers elucidate additional benefits to a number of key features of animal social living. These include an additional benefit of developing individual recognition in species with repeated interactions (e.g. horses [56], hyenas [57], primates [58], dolphins [59], rodents [60]), and for extending group tenure lengths for dispersing individuals in group-living species (e.g. hyenas [61], primates [62–65]). Consistent with this, a testable general empirical prediction from our model is that animal species in which female signal variation has a persistent underlying structure across females should be under greater selection for the development of repeated interactions and individual recognition.

Other conclusions, some of which may be more specific to systems of cyclic fertility signals, relate to how changes to conditions affect the magnitude of fitness benefits. Consistent with empirical evidence that links reproductive synchrony to the degree of reproductive skew in polygynandrous mammalian species [66,67], the effects of reproductive synchrony are important. Female reproductive asynchrony enhances the advantage of familiarity and learning, as males are able to mate with a greater number of fertile females due to their lack of synchrony, and these effects are inevitably enhanced further by increasing the number of females. This is interesting, as it suggests that it is when there are a large number of females, and when females are asynchronous, that these types of learning abilities are most favoured. It also suggests that male group residency lengths should be expected to increase due to the strong advantages of familiarity with specific females. That said, it is also in these circumstances that male competition for high-ranking positions is expected to be strongest, such that tenure lengths may be shortened by strong competition for positions and consequent male group ejection by other males. In contrast, synchrony, and low female numbers, are expected to reduce the gross benefits of learning, and of long group residency lengths. As such, our model makes testable empirical predictions for primates living in polygynandrous societies where females exhibit fertility signals. These include that primate species with greater mating synchrony (which can be inferred from birth synchrony) and with smaller group sizes will experience lower gross benefits of male learning. While a number of factors will influence male group tenure lengths, this factor should be one effect selecting for shorter tenure lengths relative to males in species with lower mating synchrony and larger group sizes. Alternatively, other factors may be more important in determining male group tenure length, with this length then determining the relative fitness benefits of learning. Moreover, males with shorter tenure lengths are predicted to develop reduced knowledge about the characteristics of specific group females relative to males in species with longer tenure lengths. Our results may also have implications for the benefits of particular male reproductive strategies. For example, in some primate species, males invest substantive amounts of time in association with specific females ('friendships' [68]). Increased close access to specific females, and the associated ability to learn their signal variation, is another potential advantage to such investment. This might be especially true for cues and signals of fertility that might be only available from close range, such as detectable changes in vaginal cytology [69].

Our model inevitably makes a number of assumptions, which can easily be modified. These include that: (i) there is an equal probability of success for all males that mate during the fertile period i.e. that no one day is more fertile than the other within the fertile phase, and that males do not differ in their fertility, nor can females exert post-copulatory mate choice via sperm discrimination; (ii) all males start on Day 1 of the simulation, when it seems likely that some males will have been present for longer than others, which is important for any Bayesian learner; (iii) measurement noise is intrinsic to the female (i.e. a probabilistic signal) and therefore equal across males. In reality, males are likely to have differential access to female signals, and also to differ in their ability to judge them.

Although not parametrized in our model, a Bayesian male could reap even more benefits by keeping track of the mating histories of each female, hence modulating the probability of success. Similarly, under conditions of synchrony, we only modelled circumstances in which the Bayesian male does not know about the degree of synchrony in ovulation time between females, but such knowledge would also further increase his advantage. As such, the advantages of being a Bayesian learner seem likely to be even greater than found in our model. Our simulations have revealed that animal receivers that learn the range of signals given by specific signallers, and place signals into that context, have very significant advantages over other individuals. Given this, further work should seek to investigate the commonality of the phenomenon empirically across a broad range of taxa and contexts in which repeated interactions and individual recognition are found.

Data accessibility. All code is available from the Dryad Digital Repository at: http://dx.doi.org/10.5061/dryad.t0680db [50].

Authors' contributions. Both authors conceived and designed the study. W.J.M. undertook the modelling, with iterative feedback from J.P.H. J.P.H. wrote the manuscript with input from W.J.M.

Competing interests. We declare we have no competing interests.

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