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The Evolution of Female Coyness – Trading Time for Information

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Abstract

Females in socially monogamous species require a period of courtship before they start to reproduce. When female reproductive success depends on male assistance, such 'coy' behaviour might have evolved in response to male philandering. In this paper, we use a dynamic optimization model to demonstrate that female coyness can be maintained during evolution (provided that a female is able to reject a male and find a new one) if two conditions are met. First, both faithful and philandering males must be present. Second, a female must be able to learn more about a male's intention by spending time with him. In our model the optimal duration of coyness is a trade-off between the benefit of waiting and gaining information about the male partner and the cost of postponing the onset of reproduction. This trade-off is influenced by several factors, such as the time needed to find a male, the level of male philandering and the possibility of detecting these males, the decline of the reproductive success with time and the disadvantage of reproducing with a philandering male.

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Introduction

In monogamous species in which males and females cooperate in reproduction, a period of courtship usually precedes reproduction. The male is usually fertile when the pair meets for the first time, while the female often needs to be stimulated by a period of male presence and courtship to start reproducing (Lehrman 1964; Bastock 1967). In pigeons, for example, 6 d of male courtship cause the ovaries to enlarge more than fourfold (Lehrman 1959). That a female, when courted by a male, is unwilling or unable to start reproduction immediately is referred to as female coyness (see, e.g. Dawkins 1976).

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How can such coy behaviour be explained? A courtship period seems to contain several costs for the female. In animals with seasonal reproduction, it is a well-known fact that reproductive success decreases with the time of start of the reproduction in the season (Klomp 1970). In addition, courtship may be energetically costly and might expose both participants to a greater risk of predation .

A classical explanation for coy behaviour is the need for the male and the female to synchronize their reproductive physiology (Bastock 1967). Whether synchronization is a problem per se is unclear since males apparently can reach a fertile state without the presence of a female (e.g. Lehrman 1959). Nevertheless, it may be advantageous for females to wait activating the reproductive physiology until meeting a male, since it might be costly to always be physiologically prepared for reproduction.

In *The Selfish Gene* Dawkins (1976) suggested that females are coy in order to avoid reproducing with philandering males. It is costly for a socially monogamous female to be deserted or end up in a polygynous situation. Several studies have shown that female reproductive success increases with the amount of male assistance (e.g. Davies & Houston 1986; Carey & Nolan 1979; Hannon & Martin 1992; Lundberg & Alatalo 1992). Conversely, a male's reproductive success might not always be maximized by helping the female. Dawkins (1976) developed a game theory model that considered this reproductive conflict between males and females. However, his game did not predict all females to be coy and it was later shown that his mixed solution was not necessarily stable (Schuster & Sigmund 1981). In this paper we suggest that Dawkins basically was correct in suggesting that female coyness may have evolved in response to male philandering, but that the game he analysed did not consider the fact that philandering and faithfulness are conditional behaviour.

There is considerable empirical evidence showing that males allocate time and energy both into co-operating with their mate and into searching for extra-pair copulations (Birkhead & Møller 1992; Andersson 1994) or trying to bond with a second female (Carey & Nolan 1979; Davies & Houston 1986; Lundberg & Alatalo 1992; Hannon & Martin 1996). In this paper we ask how a female should behave when males are both faithful and philanderers. We suggest that the female, by staying coy, gains information about the intention of a courting male and use a dynamic optimization model to investigate the conditions under which a coy female strategy is maintained.

The Model

Our task is to find the optimal time for a female to wait, once paired with a male, before starting actual reproduction (i.e. in birds the production of eggs). There are two kinds of males. The faithful male remains with the female after reproduction. The philandering male stays with the female until she either starts to reproduce or she detects and rejects him.

Let s be the pairing time and let t be the time of season. Both s and t are measured in discrete time units. Pairing time s ($s \geqslant 1$) concerns females that are paired but have not yet started to reproduce, and represents the number of time-steps they have been paired with a particular male. The rule we seek is the threshold for s, when a female will start reproducing. A female can only reproduce once. We also assume that her reproductive success declines with time in the season, thus making sure that a female does not postpone reproduction because the ecological conditions will improve later in the season. For the sake of simplicity we chose the reproductive success to decline exponentially, as e^{-rt}, with time of onset of reproduction in the season. Female reproductive success also depends on whether she reproduces with a faithful or a philandering male. If the male is unfaithful, female reproductive success is devalued with the deception factor δ ($0 < \delta < 1$).

A female may be unpaired, paired, or reproducing. An unpaired female finds a male with probability ($p_c + p_d$) during a time unit, where p_c and p_d is the probability of meeting a faithful or philandering male, respectively. An unpaired female always pairs with an encountered male. The coy period lasts from the time when the female and the male pair up until the female decides to reproduce. If the male is a philanderer she will detect this with a probability q each time-step. Once the female has detected a philanderer she will reject the male and start searching for a new one. We do not have to consider the alternatives of either starting to reproduce with the philanderer or wait another time unit. An 'optimal' female will never end up in a situation where the best alternative is to reproduce with a detected philanderer, because if that is the case she should have started to reproduce in a previous time-step. To wait is 'suboptimal' since no further information can be gained and reproductive success decreases with time. Thus, once a female detects a philanderer she rejects him and becomes unpaired again.

The probability of being paired with a faithful male at pairing time s we call $G_c(s)$ and this depends on the probability with which the female detects and rejects a philanderer at each time-step, q, as well as the proportion of philanderers, $p_d/(p_c + p_d$; see appendix). A female becomes more and more certain about a male's faithful intentions as time passes and he is not detected as a philanderer.

We calculate the optimal time for a female to wait before she allows reproduction using the technique of dynamic programming (Mangel & Clark 1988). The female has two options: start reproducing, R, or wait, W. Her choice depends on the time she has spent paired with a male, s, as well as the time of season, t. In accordance with Mangel & Clark (1988) notation, we define a fitness function F(s,t,T), where F corresponds to the maximum expected reproductive success in a breeding season at any time *t* given pairing status *s* and a breeding season of *T* time steps. This gives us the dynamic programming equation:

$$F(s,t,T) = \max(W_{s,t}, R_{s,t}) \quad t \in [0, T-1]$$

$$F(s,T,T) = 0$$

where W_{st} is the expected fitness of a female postponing reproduction in state (s,t) and R_{st} the expected fitness of a female starting reproduction in the same state.

Provided that there is optimal behaviour in time step t + 1 and beyond, W and R are calculated as:

$$W_{s,t} = \begin{cases} (p_c+p_d)F(1,t+1,T)+(1-(p_c+p_d))F(0,t+1,T) & s=0 \\ (G_c(s)+(1-q)(1-G_c(s)))F(s+1,t+1,T)+q(1-G_c(s))F(0,t+1,T) & s>0 \end{cases}$$

$$R_{s,t} = \begin{cases} 0 & s=0 \\ G_c(s)e^{-rt}+(1-G_c(s))\delta e^{-rt} & s>0 \end{cases}.$$

Note that fitness is assessed at the beginning of a time period (Mangel & Clark 1988) and that a female only gets fitness if she reproduces. Also, s = 0 refers to unpaired females.

The optimal time to stay coy was calculated varying a number of parameters: the deception factor, δ, the rate of decline of reproductive success with time, r, the probability of encountering a male ($p_c + p_d$), the proportion of philanderers, $p_d/(p_c + p_d)$, and the probability of detecting a philanderer at each time–step, q.

Results

For a given set of parameters the optimal degree of coyness is constant over the season as long as we are not close to the end of season. This result is due to the proportion of philandering males being constant throughout the season as well as the cost of postponing reproduction decreasing with a constant rate over time.

Fig. 1a shows the optimal duration of coyness as a function of the detection probability at each time-step (varied between 0 and 1) and the proportion of philanderers (varied between 0 and 1). For low values of detection probability the female tends not to be coy. The benefit of increased information about her partner's strategy is not enough to justify the reproductive cost of postponing the onset of reproduction. When the likelihood of detection increases, females have a tendency to be increasingly coy up to a point when it starts to be relatively easy to detect a philanderer. Then the degree of coyness decreases as less and less further knowledge is gained by staying coy an extra time-step. When the proportion of philanderers is low, females tend not to be coy. The female will benefit too little in comparison with the time cost she pays for avoiding the few philanderers that there are. Again, the tendency to stay coy increases to a certain point with increasing proportions of philanderers. Beyond this point there is less and less is justification of the cost paid by postponing reproduction, since faithful males become increasingly rare. In Fig. 1a the maximum value of the duration of coyness is 12 time-steps. The maximum value is found for a combination of high philanderer proportions and low detection probabilities.

A third parameter influencing the duration of coyness is the rate of decline of reproductive success with time, r. An increase in the cost of postponing reproduction, increasing r from 0.01 to 0.04, results in a lower tendency to stay coy. The maximum degree of coyness also decreases from 12–two time steps (compare Fig. 1a and b). An increased decline of reproductive success with time is an incentive

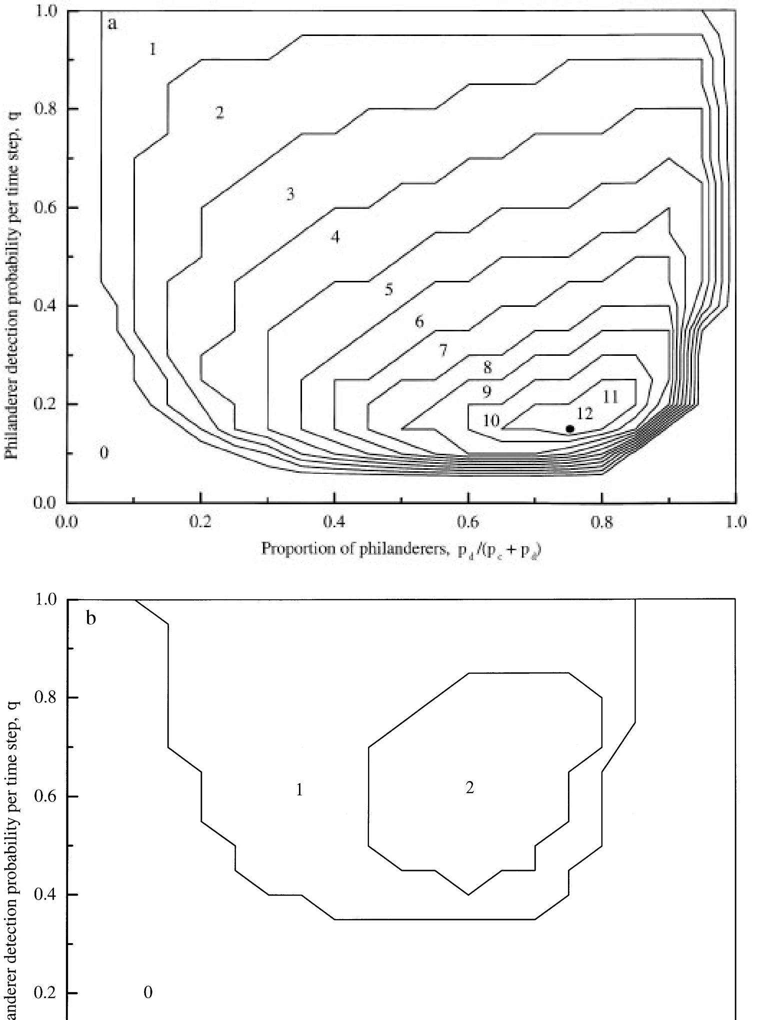

Fig. 1: a. The optimal duration of coyness as a function of the female's philanderer detection probability, q, and proportion of philandering males, $p_d/(p_c + p_d)$; $r = 0.01$, $\delta = 0.5$ $(p_c + p_d) = 0.6$. The numbers given in the figure represent time-steps of optimal coyness within the areas defined by contour lines. Note that being coy for 12 time-steps is only optimal in a very small area (black dot). Generally speaking, when the proportion of philanderers increases, it pays the female to be more coy, and when the probability of detecting a philandering male increases the female can afford to be less coy. b. If the reproductive success declines more sharply with time, i.e. r increases, and it is costlier to postpone reproduction, the female will be less coy; here $r = 0.04$, $\delta = 0.5$, $(p_c + p_d) = 0.6$ (compare a and b). c. When the female is more dependent on male help, i.e. δ decreases, and the cost of deception increases, it pays her to be more coy; here $r = 0.04$, $\delta = 0.25$, $(p_c + p_d) = 0.6$ (compare c and b). d. When the probability of finding a male decreases, i.e. $p_c + p_d$ decreases, females become less coy; here $r = 0.01$, $\delta = 0.5$, $(p_c + p_d) = 0.1$ (compare d and a)

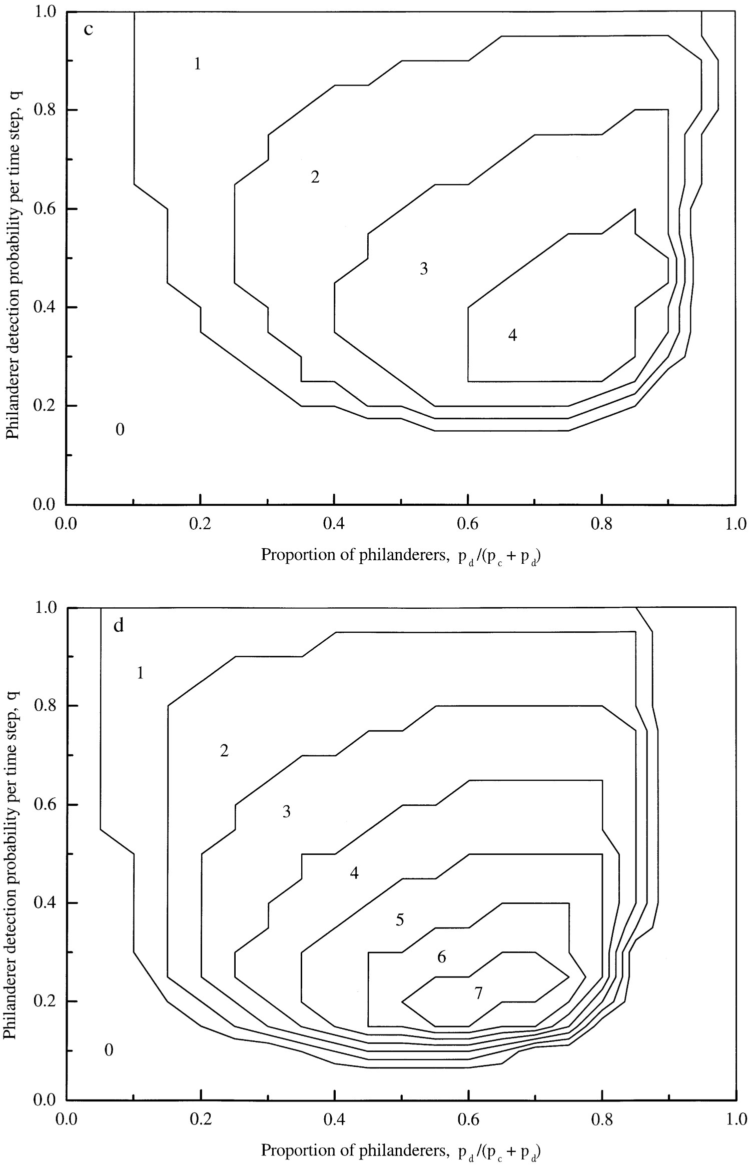

Fig. 1: Continued

for starting to reproduce sooner. The demand on the benefit of waiting increases as the cost of postponing reproduction increases. More information has to be gained in every extra waiting time for coyness to pay.

If the cost of reproducing with a philanderer increases, i.e. decreasing δ from 0.5 to 0.25, the maximum duration of coyness increases from two to four time-steps (compare Fig. 1b and c). If the female becomes more dependent on male help it pays the female to be coyer.

A fifth parameter of importance is the probability of finding a male. Lowering the probability of meeting a male ($p_c + p_d$) from 0.6 to 0.1, the optimal time to stay coy decreases. The maximum duration of coyness decreases from twelve to seven time units (compare Fig. 1a and d). Once the female has found a male it will take a considerable amount of time to find a new male if the present one is rejected. The rare help from a philandering male is still better than time-consuming searches for the few faithful males.

Discussion

Our results show that coyness can be explained as a female strategy against philandering males. The longer the female waits with her reproduction in the season the lower her reproductive success will be. Conversely, the longer the female stays coy, the more certain she may become of the male's intentions. In the model, a female's strategy evolves as a trade-off between the benefit of gaining information and the cost of postponing reproduction. This trade-off is influenced by the time needed to find a male, the level of male philandering, the possibility of detecting such males, the variation of reproductive success with time, and the disadvantage of reproducing with a philandering male. We have used the term coy following Dawkins' (1976) terminology. The term may be partly misleading since the fact that the female is coy does not exclude her from being sexually active before becoming fertile, something that is commonly observed in many species (e.g. Lehrman 1964; Birkhead et al. 1987; Sever & Mendelssohn 1988; Birkhead & Møller 1992).

A pure coy female strategy can be maintained if three conditions are met. First, both faithful and philandering male behaviour must be present. As mentioned in the introduction, there is ample evidence that males, while cooperating with a particular female also regularly court other females without the intention of associating with them. Second, the female must be able to assess a male's intention by spending time together with him. For example, a male that already is paired will not be able to show a new female as much attention as an unpaired male with faithful intentions (e.g. Stenmark et al. 1988; Temrin & Arak 1989). Thus, a female might avoid reproducing with a philanderer by only accepting males that have spent considerable time with her. Another possibility of uncovering a male that already is paired, is to spot his mate (e.g. Breiehagen & Slagsvold 1988). Third, a female must have the possibility of rejecting a male and finding a new one.

In this paper we have only considered the behaviour of the female. The proportion of philanderers as well as the probability of finding males remains constant during the whole season. These assumptions are chosen for the sake of simplicity. However, this is a game between males and females and the proportion of philandering males is likely to vary during the season. It is important that the defence against philandering does not become too efficient, as that could lead to a rapid drop in male philandering (Enquist & Leimar 1993). This is the case in

Dawkins's (1976) model. How do we maintain both male types in the population? One way out of this problem would be if some males still gain from philandering when females start to turn coy. In socially monogamous species, a male that already has a female might still benefit from philandering with new females, when females are coy. A male might also start off as a philanderer and later in the season become faithful or vice versa. For example, in the pied flycatcher, *Ficedula hypoleuca*, about two-thirds of the males try to attract a second female. Not all of these succeed, but about 10–15% of the females ends up reproducing as secondary females (Lundberg & Alatalo 1992).

Although Dawkins' (1976) model of coyness correctly proposes female coyness as a defence against unfaithful male strategies it suffers from a few problems. First, both types of males might not always be present, which is a requisite for maintenance of coyness. Second, a male exposes his intentions immediately in Dawkins' game, which makes it meaningless to stay coy and lose precious time. Third, it is worse to reproduce with a philanderer than not to reproduce at all — something that is not necessarily true. This last is needed because the game occurs in one time-step only. Thus, females cannot search for a new male.

Our results might also be relevant in other biological contexts where cooperators risk being exploited by defectors. For example, simultaneous hermaphrodites can be considered to engage in reproductive cooperation, where individuals in such populations might allocate more resources to the female sex and egg production, producing only the amount of sperm necessary to fertilize the partner's eggs. All individuals gain from this cooperation. The problem is that an individual that puts more reproductive resources into producing sperm instead of the costlier eggs might have a greater reproductive success than other individuals, cheating the partners on the access to eggs. Analogous to the development of coy behaviour in socially monogamous species, simultaneous hermaphrodites should have evolved a number of efficient defences against non-cooperative male-like strategies. Empirical evidence also indicates that simultaneous hermaphrodites typically engage in time-consuming and complex copulation acts (e.g. Fischer 1980, 1984; Pressley 1981; Tompa et al. 1984; Leonard & Lukowiak 1985; Fischer & Hardison 1987; Sella 1988; Ockelmann & Åkesson 1990), possibly increasing the probability of exposing cheating individuals. For example, the pulmonate gastropod *Helix pomatia* engages in simultaneously reciprocal copulation and it is not until both partners simultaneously succeed in an intromission that the copulation phase can start. The whole act might take up to 9 h (Jeppesen 1976). These relatively costly behaviours could not be evolutionary maintained without the presence of some defection in the populations. An individual that had already engaged in a cooperative interaction might attempt to cheat a new individual trying to fertilize its eggs, without offering eggs in return. A few studies indicate that such cheating is present in the population (Fischer 1980; Sella 1988).

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Appendix

Probability of being paired to a faithful male at pairing time s, $G_c(s)$:

$$G_c(s) = \begin{cases} \dfrac{p_c}{p_c + p_d} & s = 1 \\[2ex] \dfrac{p_c}{(p_c + p_d)(1-q)^{s-1} + p_c q \sum_{j=0}^{s-2} (1-q)^j} & s \geqslant 2 \end{cases}$$