

Decision making and recognition mechanisms

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Determining how individuals adjust their behaviour to maximize reproductive opportunities is fundamental to understanding the adaptive significance of behavioural variations. Such ‘decision making’ requires recognition mechanisms, whereby an individual evaluates cues that yield information about the potential reproductive outcomes of alternative behaviours. Here, we develop a quantitative model for understanding how individuals evaluate cues. Only when a proximate (immediate) cue predicts reproductive value more reliably than an evolved predisposition, will the cue influence an individual’s decision. The model resolves some long-standing controversies in evolutionary biology involving recognition mechanisms and interpretations of behavioural decisions that were observed after manipulations of cues of parentage, kinship and mate quality.

Keywords: decision making; recognition; perception; parentage; parental investment; Bayes’ rule

1. INTRODUCTION

We sought to develop a general model of decision making. To do so we focused initially on a specific, controversial example from evolutionary biology: parentage and parental investment (Trivers 1972; Whittingham *et al.* 1992; Westneat & Sherman 1993; Kokko 1999; Sheldon 2002). A key prediction from parental investment theory is that genetic relatedness to young (parentage) should affect an individual’s parental efforts. When relatedness to a brood is decreased by cuckoldry or intraspecific parasitism, the evolutionary value of investing in those young is decreased. Cuckolded or parasitized parents should reduce effort toward the current brood in favour of alternative investments (i.e. in future broods) whenever the alternatives are expected to provide greater reproductive success. This is known as ‘Williams’s principle’ (Sargent & Gross 1993).

Several correlative studies have reported the predicted association between parentage and parental care (e.g. Burke *et al.* 1989; Dixon *et al.* 1994; Neff & Gross 2001). However, there is controversy about how to interpret these studies since they do not control for all potential confounding phenotypic or life-history correlates (Lessells 1991; Jamieson & Quinn 1997; Kempenaers & Sheldon 1997; Lifjeld *et al.* 1998b; see also Kokko & McRae 2000). For example, a male that has high paternity in his social mate’s brood may also have a good territory and be in fine condition, and therefore able to invest in parental care. Thus, the apparent association between paternity and parental investment may be due to the male’s quality and circumstances instead of his assessment of parentage.

To control for such confounding effects, experimental manipulations of perceived parentage have been advocated (Lessells 1991; Kempenaers & Sheldon 1997) and conducted. Certain results support the theory (Møller 1988, 1991; Davies *et al.* 1992; Wright & Cotton 1994;

Lifjeld *et al.* 1998a; Sheldon & Ellegren 1998; Osorio-Beristain & Drummond 2001) while others do not (Whittingham *et al.* 1993; Sheldon *et al.* 1997; Kempenaers *et al.* 1998; MacDougall-Shackleton & Robertson 1998; Svensson *et al.* 1998). Contradictory results have led some authors to question the utility of the experiments and others to doubt the appropriateness of the theory (reviewed by Wright 1998; Sheldon 2002). Here, we develop a framework to integrate these heterogeneous results and resolve the controversy.

2. THE MODEL

Our framework focuses on how individuals perceive cues when evaluating the reproductive consequences of behavioural options. Like all decision-making processes, adaptive parental investment requires that individuals can evaluate these outcomes accurately (Williams 1966; Sherman *et al.* 1997; Shettleworth 1998). Assessments are based on *proximate cues* and *predispositions*, as well as the evolved mental processes for weighing them (i.e. the Darwinian algorithms: Wiley 1983; Cosmides & Tooby 1987; Reeve 1989; Sherman *et al.* 1997). A proximate cue is one that is immediately being evaluated by an individual. A predisposition is any previous (relative to the proximate cue) information that an individual has regarding an assessment. The predisposition includes information gained during the individual’s lifetime, but it is shaped through evolutionary time. For example, imagine a species in which the probability of being cuckolded is consistently low early in the breeding season but variable later on. Early in the season, a male can be sure that he sired his mate’s offspring, regardless of such proximate cues as his frequency of copulation or time spent alone with or away from his mate. Thus, early-breeding males have strong predispositions of high parentage, and they can safely ignore proximate cues. By contrast, late-breeding males must rely on proximate cues since they have no accurate predisposition to assess parentage. Our model therefore

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focuses on the effects of proximate cues and predispositions on perception.

To evaluate independent proximate cues in conjunction with a predisposition, we apply Bayes's rule (e.g. see Bradbury & Vehrencamp 1998; Lewis 2001) and define the following conditional probability:

$$\Pr(\beta | \mathbf{cue}) = \frac{\Pr(\beta) \prod \Pr(\text{cue}_i | \beta)}{\Pr(\mathbf{cue})}, \quad (2.1)$$

where β is an index of the possible values of parentage. β can take on any value between zero (no young belong to the parent) and unity (all young belong to a parent); fractional values of β occur when not all of the young are offspring of the parent or when they are offspring of kin.

The values of the proximate cues are contained in the vector \mathbf{cue} . For example, if the male evaluated the time he spent alone with his fertile mate and his copulation frequency, then \mathbf{cue} would have two components (cue_1 and cue_2). $\Pr(\text{cue}_i | \beta)$ is called the reverse probability, and it relates parentage to the cues. When a proximate cue is reliable the reverse probability is approximately zero for any value of β that is not close to the parent's actual parentage. For example, suppose that a male copulated with a female once per hour during her fertile period and fertilized 80% of her eggs. When copulation frequency is reliable the probability of copulating once per hour given a parentage of 80% is high, while the probability of copulating once per hour given any other parentage is low. Reliability reflects how precisely the cue conveys information about parentage. Thus, a male's copulation frequency is a reliable cue if copulation frequency is tightly correlated with parentage (figure 1a) and an unreliable cue if it is not (figure 1b).

$\Pr(\beta)$ is the prior probability and represents the predisposition. *Strong* predispositions are reliable, implying that the variance in the prior probability $\Pr(\beta)$ is small (relative to the range of values for β), whereas *weak* predispositions are unreliable (i.e. the variance in $\Pr(\beta)$ is large). $\Pr(\mathbf{cue})$ is the probability of observing the cues independent of parentage. Thus, Bayes's rule incorporates the influence of both proximate cues and predispositions, and provides the appropriate framework for understanding recognition and assessments.

When multiple cues are analysed which are not independent, an analogous equation to (2.1) can be generated

$$\Pr(\beta | \mathbf{cue}) = \frac{\Pr(\beta) \prod \Pr(\text{cue}_i | \beta, \text{cue}_{j < i})}{\Pr(\mathbf{cue})}, \quad (2.2)$$

where all variables are defined as earlier. Here, the reverse probability is conditioned on not only β , but also all previous cues ($j < i$). For example, if there were two dependent cues, then the reverse probabilities in equation (2.2) would be: $\Pr(\text{cue}_1 | \beta) \times \Pr(\text{cue}_2 | \beta, \text{cue}_1)$. It is arbitrary which cue is specified as the first. If the two cues were in fact independent then $\Pr(\text{cue}_2 | \beta, \text{cue}_1) = \Pr(\text{cue}_2 | \beta)$ and equation (2.2) is equivalent to equation (2.1).

$\Pr(\beta | \mathbf{cue})$ is the conditional probability from which an individual can 'calculate' its parentage based on the proximate cues it has assessed. This can be done mathematically by generating a probability distribution for each possible value of β (i.e. parentage = 0–1), and the expected value of β (i.e. an individual's perceived parent-

age or 'best guess' of what its parentage is) is calculated from

$$\bar{\beta} = k \int_0^1 (\Pr(\beta | \mathbf{cue}) \beta) d\beta, \quad (2.3)$$

where k is the normalization constant defined such that $k \int \Pr(\beta | \mathbf{cue}) d\beta = 1$. The expected value of β provides an unbiased estimate of an individual's parentage.

The parental investment (PI) made by an individual (e.g. amount of food delivered to the young) will depend on the net benefits (ω) of the investment. This in turn depends on the probability of parentage (equations (2.1) or (2.2)) and any other variable affecting the value of the current brood (e.g. offspring number or quality) relative to the benefits from other investment options (e.g. future mating opportunities). This is referred to as the opportunity cost of investment from which the optimal investment (PI*) can be calculated (e.g. see Whittingham *et al.* 1992). Manipulation of perceived parentage (β) over a range in which $d\omega/d\beta \cong 0$ will have only a small effect on PI*, while manipulation of perceived parentage over a range in which $|d\omega/d\beta| \gg 0$ will have a large effect on PI* (Whittingham *et al.* 1992).

3. RESULTS AND DISCUSSION

If an individual does not have a strong predisposition about its parentage, but a reliable proximate cue is available, then perceived parentage will depend on that cue (figure 2a). Conversely, if an individual has a strong predisposition, proximate cues will have little influence on its investment decision, even if the cue independently indicates substantially different parentage from the predisposition (figure 2b). When multiple proximate cues are evaluated, each will contribute to perceived parentage (equation (2.2)). All else being equal, the influence that any one cue has on the assessment increases with its reliability and decreases with the number of cues used.

Field tests of decision-making processes generally focus on manipulating a single proximate cue. However, in order for cue manipulation to alter perceptions:

- (i) individuals must not have a strong predisposition (relative to the reliability of the proximate cue); and
- (ii) the appropriate (evolutionarily reliable) proximate cue or cues must be manipulated.

In the case of parental investment there is considerable variability in the outcomes of cue-manipulation experiments: whereas certain results lend support to the theory, others seem inconsistent with it (e.g. Wright 1998; Sheldon 2002). Of course, it is conceivable that parentage actually had little effect on optimal parental investment (i.e. $d\omega/d\beta \cong 0$) in the studies which failed to find an effect of a cue manipulation (Whittingham *et al.* 1992; but see Westneat & Sherman 1993; Houston 1995). However, it is more probable that different outcomes occurred because either the proximate cue chosen for manipulation was not a reliable indicator of parentage or individuals had evolutionary predispositions about parentage that overrode that cue (table 1).

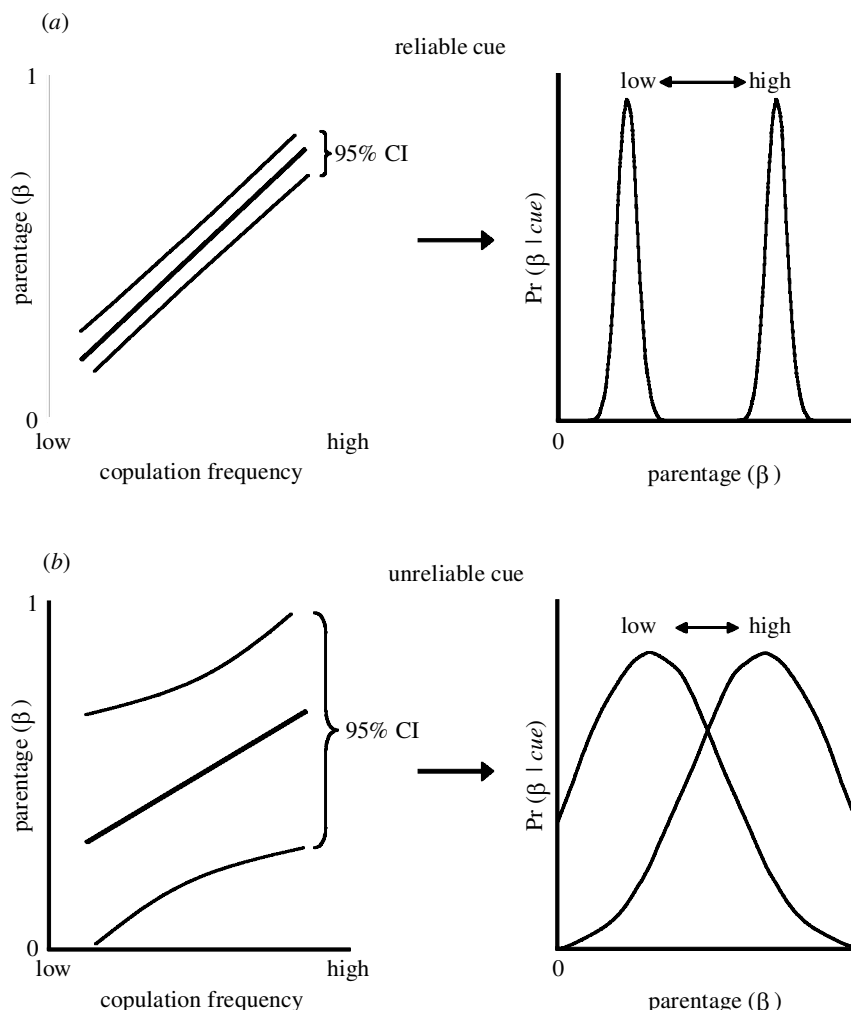


Figure 1. Reliable and unreliable cues of parentage. Reliability is determined by the strength of the correlation between the cue and parentage. (a) A reliable cue is highly correlated with parentage (left) and therefore has a narrow probability distribution relating the cue to parentage (right). (b) An unreliable cue is weakly correlated with parentage (left) and therefore has a broad probability distribution relating the cue to parentage (right). As an example, a male that has a high-copulation frequency with his mate can be sure he has high paternity if the cue (copulation frequency) is reliable, but he cannot be sure otherwise. CI, confidence interval.

For example, consider dunnocks (*Prunella modularis*). These small passerines have a variable mating system which includes socially monogamous pairs and polyandrous trios (Davies 1992). The latter involves an alpha and beta male that both copulate with one female. Being alpha does not necessarily predispose a male to high paternity, nor does being beta necessarily mean low paternity (beta males fertilized an average of 44% of young, range = 0–100%: Davies *et al.* 1992). Instead, paternity is determined by the proportion of time each male spends alone with the female (i.e. guarding and mating; Davies *et al.* 1992). In our terminology, a male's exclusive access time is a reliable proximate cue of paternity. Under our model, manipulation of this cue should affect perceived parentage and parental investment (figure 2a). Indeed, Davis *et al.* (1992) found that capturing and detaining alpha males briefly during egg laying, when their female was fertile, resulted in a significant decrease in the males' paternal efforts.

By contrast, when male and female dunnocks pair monogamously, males are rarely cuckolded (e.g. they sired all 49 chicks across 15 nests in one study: Burke *et al.* 1989).

Capturing and briefly holding socially monogamous males during egg laying had little effect on their paternity (e.g. 10 of 15 nests had no reduction in paternity: Davies *et al.* 1992). Thus, an exclusive pairbond typically is a reliable cue to a male of high paternity, whereas temporary separation from his pairbonded mate is not a reliable cue that his paternity has been compromised. As expected under our model (figure 2b), detaining socially monogamous males during egg laying did not affect (reduce) their subsequent paternal efforts (Davies *et al.* 1992).

A second example comes from studies of barn swallows (*Hirundo rustica*). These birds sometimes nest colonially and sometimes as isolated pairs. In the colonial situation extra-pair fertilizations are common, but the frequency of extra-pair chicks is not related to a male's arrival date at the breeding area or his physical condition, song rate or parasitic load (Møller 1988, 1991). Thus, males have no obvious basis for any predisposition about paternity. However, parentage of colonial males is highly correlated with males' effectiveness in guarding their social mate against sexual assaults by other males (Møller 1988, 1991). Guarding efficacy thus is a reliable cue of parentage. As

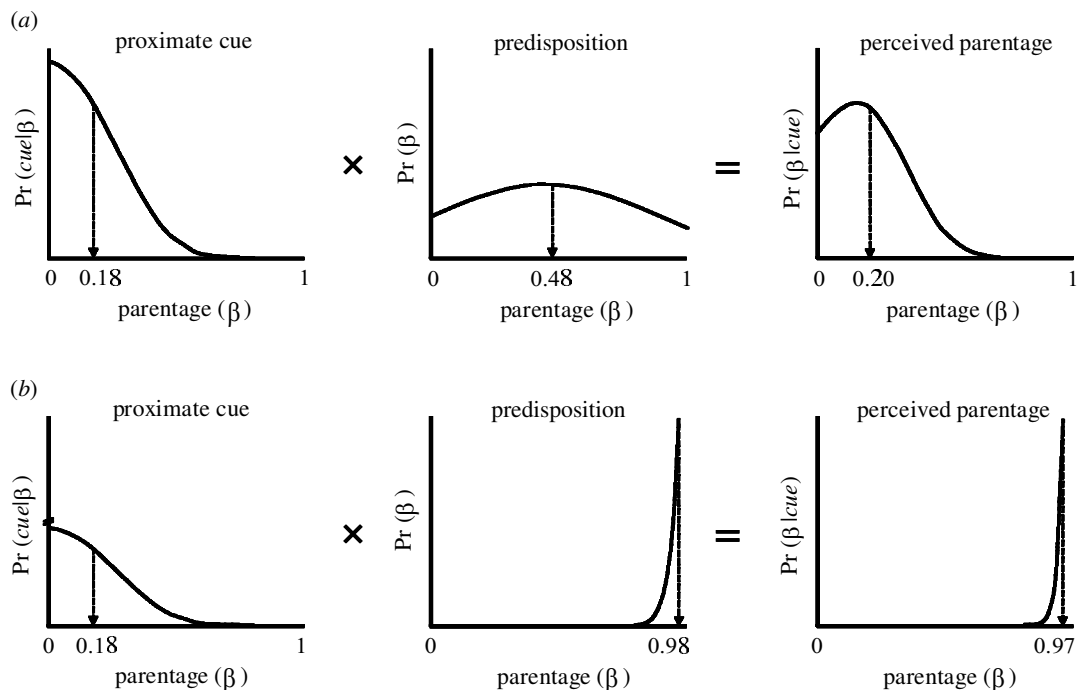


Figure 2. The effect of manipulating a cue on perceived parentage in dunnocks. (a) When proximate cues are reliable and only a weak (unreliable) predisposition exists, the former largely determines an individual's perceived parentage. This example is based on polyandrous dunnocks. The proximate cue is the proportion of exclusive mating access and the predisposition is based on status (alpha versus beta). The proximate cue indicates a parentage of 18%, the predisposition indicates 48% and the perceived parentage is 20%. (b) When a strong (reliable) predisposition exists, proximate cues have little influence on the perceived parentage of an individual. This example is based on monogamous dunnocks. The predisposition is based on mating type (monogamous versus polyandrous) and in nature provides a reliable cue of parentage. No reliable proximate cue exists. Even when one assumes a cue with similar reliability to the proximate cue used by polyandrous dunnocks that indicates a parentage of 18%, the strong predisposition indicates 98% and the perceived parentage is 97%. Generally, the effect of the proximate cues on perceived parentage is inversely related to the variance in the reverse probability distribution (proximate cue) relative to the variance of the prior probability distribution (predisposition). The equations used to generate the distributions are presented in Appendix A.

expected (e.g. figure 2a), colonial-breeding males that were briefly detained during their mate's fertile period provided less parental care than 'control' males that were detained after egg laying was over (Møller 1988, 1991).

By contrast, when barn swallows nest as isolated pairs, extra-pair fertilizations rarely occur. Even temporary male removal during egg laying does not diminish paternity (Møller 1988). Nesting in isolation is therefore a reliable cue of high paternity, and provides males with a predisposition, whereas temporary separation is unreliable as a cue that paternity has been compromised. Not surprisingly under our framework (e.g. figure 2b), therefore, solitary-nesting males did not change their rates of feeding chicks regardless of whether they were briefly held captive during their mate's fertile period (Møller 1988).

Our approach also provides insights into some puzzling behaviours that have been observed in other decision-making contexts, such as recognition of kin and high-quality mates. Regarding the former, when newborn pups of golden hamsters (*Mesocricetus auratus*) (Mateo & Johnston 2000) and Belding's ground squirrels (*Spermophilus beldingi*) (Holmes & Sherman 1982; Holmes 1986) were experimentally cross-fostered into unrelated litters, both they and 'control' pups (reared by their genetic mother) treated rearing mates as siblings when they reached sexual maturity. This indicates that kin recognition is mediated by social learning in both species. However, cross-fostered

hamsters and Belding's ground squirrels could discriminate among non-nest-mates based on relatedness. They distinguished siblings from non-siblings among individuals that were reared in other nests. In nature, juveniles that are reared in the same nest or burrow always are kin (either full-siblings or maternal half-siblings), but juveniles reared in neighbouring burrows are not always non-kin (i.e. due to male polygyny, they might be paternal half-siblings). Thus, individuals have a reliable predisposition to accept nest-mates as relatives regardless of their proximate cues (e.g. figure 2b), but they have no reliable predisposition for rejecting all non-nest-mates as non-relatives (e.g. figure 2a). In order to discriminate among non-nest-mates they must use reliable (genetically determined) proximate cues to assess the similarity of the foreign individual to themselves or their nest-mates. Chemical cues are likely, because odour differences correlate with relatedness (Mateo & Johnston 2000; Mateo 2002).

Finally, consider mate-quality recognition in the black grouse (*Tetrao tetrix*). Only high-quality males can defend central territories on mating arenas, whereas peripheral territories are occupied by males of variable quality. Residence on a central territory reliably indicates male quality (Höglund *et al.* 1994; Kokko *et al.* 1998). Males have tail ornaments (lyres) that they display to females during courtship, and lyre size also correlates with male quality (Höglund *et al.* 1994; Rintamaki *et al.* 1997). Manipu-

Table 1. Summary of studies of parentage and parental investment (PI) involving cue manipulations. (In all cases where the proximate cue was reliable and no reliable predisposition existed, the manipulation had the expected negative effect on PI. When a reliable predisposition existed or an unreliable proximate cue was manipulated, no effect on PI was observed.)

species	proximate cue		predisposition			effect on PI	reference
	character examined	reliability ^a	characters examined	reliability ^a	manipulation		
barn swallow (colonial)	male copulation rate	reliable	male condition, arrival date, song rate, parasites	unreliable	male detention	yes	Møller (1988, 1991)
dunnock (polyandrous)	male copulation rate	reliable	male status (alpha or beta)	unreliable	male detention	yes	Davies <i>et al.</i> (1992)
European starling	time spent with mate	reliable	exclusive pairbond	unreliable	female detention	yes	Wright & Cotton (1994)
collared flycatcher	timing of removal	reliable	hatching date, brood size	unreliable	male detention	yes	Sheldon <i>et al.</i> (1997); Sheldon & Ellegren (1998)
pie'd flycatcher	time spent with mate	reliable	exclusive pairbond, hatching date, male quality	unreliable	female detention	yes	Liffeld <i>et al.</i> (1998a)
blue-footed booby	time spent with mate	reliable	male size, distance to neighbour	unreliable	male detention	yes	Osorio-Beristain & Drummond (2001)
tree swallows	time spent with mate	reliable	none	unknown	male detention	yes or no ^b	Whittingham <i>et al.</i> (1993)
barn swallow (solitary)	male copulation rate	unreliable	solitary nesting	reliable	male detention	no	Møller (1988)
dunnock (monogamous)	male copulation rate	unreliable	exclusive pairbond	reliable	male detention	no	Davies <i>et al.</i> (1992)
eastern bluebird	time spent with mate	unreliable	none	unknown	female detention	no	Kempnaers <i>et al.</i> (1998); MacDougall-Shackleton & Robertson (1998)
common goby	presence of sneaker male	unreliable	none	unknown	male detention	no	Svensson <i>et al.</i> (1998)

^a Reliability was assessed based on either quantitative data such as the effect of the manipulation on the genetic paternity of the focal male or qualitative data such as biological inference (e.g. the time a male spent with his mate was considered to be a reliable proximate cue for species with mate guarding; see references for details).

^b Parental investment measured by male dive rate to brood threat was marginally significant ($p = 0.06$); other measures of PI were not.

lation of lyre size had no effect on attractiveness of central males, but did affect attractiveness of males that held peripheral territories (Höglund *et al.* 1994). Interpreted under our model, females are predisposed to consider central males as being of high quality regardless of phenotypic cues (e.g. figure 2*b*), whereas females must assess quality of peripheral males by comparing their lyres (e.g. figure 2*a*).

4. CONCLUSION

For individuals to make adaptive decisions, they must be able to evaluate the reproductive value of behavioural options. We present a framework for understanding which cues should be used when assessing reproductive value. Our model and supporting examples (table 1) yield a simple, compelling message: studies of recognition involving manipulations of phenotypic cues will be interpretable as tests of evolutionary models of decision making and their underlying Darwinian algorithms only when the manipulations target cues that are known to be reliable in species that use those cues in decision making.

This work was supported by the Natural Science and Engineering Research Council of Canada (B.D.N.) and by the National Science Foundation and the Agricultural Experiment Station at Cornell University (P.W.S.). Helpful comments were provided by S. M. Flaxman, M. R. Gross, J. Repka, D. Tarpay, D. F. Westneat, and especially H. K. Reeve. Two anonymous reviewers also provided valuable suggestions.

APPENDIX A: ESTIMATING THE PROBABILITY DISTRIBUTIONS FOR THE PROXIMATE CUES AND PREDISPOSITIONS IN DUNNOCKS

(a) *Polyandrous dunnocks*

(i) *Predisposition*

From Davies *et al.* (1992), beta males fertilized an average of 0.44 ± 0.42 (s.d.) of the chicks in clutches (range = 0–100%; $n = 28$). In our analysis we therefore assumed that the predisposition of parentage (for a beta male) followed a normal distribution with mean of 0.44 and standard deviation of 0.42 as follows:

$$\Pr(Par) = 1.247e^{-2.834(Par - 0.44)^2}. \quad (A 1)$$

Thus, being alpha or beta does not predispose a male to high or low parentage (see figure 2*a*).

(ii) *Proximate cue*

From Davies *et al.* (1992) we extracted the data relating paternity of beta males (Par) to their proportion of exclusive mating access (Acc), from which linear regression was used to generate the following equation: $Acc = 0.07 + 0.468 \times Par$. For simplicity, we assumed that the ‘error’ around the regression line followed a normal distribution with mean ($\mu_{Par} = Acc$) and standard deviation (σ) of 0.065 (the error in the y -intercept). This error distribution was used to calculate the probability of observing a cue for each possible paternity. Specifically we modelled a scenario where exclusive mating access of the beta male was manipulated to not exceed 0.2 (or equivalently the

alpha male was given at least 80% exclusive mating access). This might be accomplished by temporarily detaining each male for an appropriate length of time. The probability of gaining up to 20% mating access given a particular paternity could then be calculated from

$$\Pr(cue \leq 0.2 | Par) = \int_0^{0.2} \frac{k_{Par}}{\sqrt{2\pi\sigma^2}} e^{-\frac{(cue - \mu_{Par})^2}{2\sigma^2}} dcue, \quad (A 2)$$

where both the normalization constant k and the mean μ were dependent on paternity (defined earlier). Here, equation (A 1) was evaluated in 0.01 increments of Par and the following normal curve was fit to the resultant data ($r^2 > 0.95$; data not shown) as follows:

$$\Pr(cue \leq 0.2 | Par) = 3.568e^{-10Par^2}. \quad (A 3)$$

Equation (A 3) therefore represents the proximate cue distribution assuming a male has up to 20% exclusive mating access to its polyandrous mate. It assumes that males are able to accurately assess mating access and may therefore be conservative (i.e. there may in fact be additional error in the assessment of exclusive mating access). Equations (A 1) and (A 3) were combined using equation (2.1) and the perceived parentage was calculated using equation (2.3) (see figure 2*a*).

(b) *Monogamous dunnocks*

(i) *Predisposition*

From Burke *et al.* (1989), monogamous males in nature fertilized all 49 chicks across 15 clutches. We assumed that each egg represented an independent fertilization event and used the binomial theorem to estimate the predisposition of monogamous males

$$\Pr(Par) = 50Par^{49}. \quad (A 4)$$

Thus, monogamous males are rarely cuckolded and will have a strong predisposition (see figure 2*b*).

(ii) *Proximate cue*

Given that monogamous males are rarely cuckolded in nature, it is difficult to imagine a reliable proximate cue of parentage and none appears to exist (Burke *et al.* 1989; Davies *et al.* 1992). We therefore modelled the effects of manipulating a mock cue equivalent in reliability to the proximate cue presented in equation (A 3). Equations (2.1) and (2.3) were again used to calculate the perceived parentage (see figure 2*b*).

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.