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Older males signal more reliably

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The hypothesis that females prefer older males because they have higher mean fitness than younger males has been the centre of recent controversy. These discussions have focused on the success of a female who prefers males of a particular age class when age cues, but not quality cues, are available. Thus, if the distribution of male quality changes with age, such that older males have on average genotypes with higher fitness than younger males, then a female who mates with older males has fitter offspring, which allows the female preference to spread through a genetic correlation. We develop a general model for male display in a species with multiple reproductive bouts that allows us to identify the conditions that promote reliable signalling within an age class. Because males have opportunities for future reproduction, they will reduce their levels of advertising compared with a semelparous species. In addition, because higher-quality males have more future reproduction, they will reduce their advertising more than low-quality males. Thus, the conditions for reliable signalling in a semelparous organism are generally not sufficient to produce reliable signalling in species with multiple reproductive bouts. This result is due to the possibility of future reproduction so that, as individuals age and the opportunities for future reproduction fade, signalling becomes more reliable. This provides a novel rationale for female preference for older mates; older males reveal more information in their sexual displays.

Keywords: sexual selection; handicap signalling; life-history theory

1. INTRODUCTION

Fisher (1958) first suggested that female preferences for male displays might increase the likelihood of mating with a high-quality male. Other authors suggested that females could choose males because they would receive some benefit (O'Donald 1962; Williams 1966), but it was Zahavi's (1975) seminal paper that introduced the idea that unconstrained, yet costly, male display could be a reliable indicator of male quality. Zahavi (1977) suggested that if male display is costly, and costlier for lower-quality males, then even though low-quality males may be physically able to produce a large display, only high-quality males will be selected to do so. These ideas were formalized in a game theoretic framework by Grafen (1990).

It is important to note that Grafen's results depend on differences in the marginal cost of signalling and do not necessarily imply that higher-quality males will pay larger absolute survivorship costs (Getty 2002). Grafen's model implicitly assumes that the life history of advertising males can be divided into a pre-breeding period, during which a male pays for advertising in mortality, and a breeding period, during which no mortality occurs.

This framework makes two simplifying assumptions. First, while male survivorship is derived as the measure of quality that determines male display, it is assumed to be correlated with the measure of utility to females (Proulx 2001*a*). Second, the life history is collapsed into a single breeding period where all costs are paid up front. This paper examines how the handicap criterion of costlier displays for lower-quality males is translated to organisms with multiple reproductive bouts; a later paper will explore how the timing of costs affects signalling (Proulx & Day 2002).

We are interested in the reliability of signals because these have an important part in determining the evolutionary stability of signalling systems and because correlations between some measure of male signal and male quality are often measured. We will refer to a male signalling strategy as reliable if the signal is an increasing function of quality within an age class. This definition of reliable signalling is intended to reflect characters that might be measured and does not imply that this form of reliability is necessary for female preferences to be beneficial. When signalling is reliable, and male quality is correlated with the utility of males as mates to females, then females can always increase their reproductive success by using the signals to make mating decisions (Proulx 2001*a*).

In Grafen's (1990) derivation of the handicap criterion the life history is implicitly assumed to be semelparous; fitness is the probability of surviving, while bearing the cost of a display trait, to a reproductive bout multiplied by the mating success achieved during that bout. Recent work by Getty (1998) draws a distinction between the costs of signalling and the fecundity benefits of signalling. For instance, high-quality males may spend more time at a lek, so that for a given level of display the high-quality male receives more matings. Thus, if high-quality males received more benefit for a given level of display than low-quality males, costly signalling could evolve even when the costs of display do not depend on quality. Getty suggests that life-history considerations can cause the benefit of male display to be condition dependent.

In one sense, all life histories can be collapsed into the expected time spent breeding, so that fitness can be expressed in the form used in Grafen (1990). However,

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lifetime breeding success is difficult to measure, and most studies measure survival probabilities over discrete intervals (Mappes *et al.* 1996; Jennions *et al.* 2001). Thus, even when lifetime fitness can be calculated as the product of a generalized survivorship and mating success, it is not easily conceptualized or translated to empirical studies.

Finally, display and mortality can change with age, making it impossible to model as a semelparous life history. The optimal male display, like any life-history allocation decision, will represent a balance between current reproductive success and future reproductive success. Because life-history trajectories are generally condition dependent (Stearns 1992), we expect the trajectory for male display to be condition dependent. The central issue of this paper concerns understanding which life histories and signal cost structures will produce reliable signalling for males of each age class.

Previous studies have touched on this issue by investigating how male advertising and mating effort strategies should change as individual males age (Kokko 1997, 1998*a*). Any factor that causes a residual male fitness to vary with age can lead to an optimal signalling allocation pattern that depends on age. Kokko (1997) developed a model where individual males can allocate resources to signalling or to increasing condition (i.e. growth) and compete at each age for mates. The model had a maximum age and examined, among other things, how changing opportunities for growth alter signalling. Kokko (1997) showed examples without growth where younger males signalled less than older males, and examples with growth where younger individuals produced larger signals.

In these sorts of models, male display is a function of both age and quality, so it is common for low-quality males of some age classes to signal at higher rates than high-quality males from other age classes. This can still lead to a signalling equilibrium if, on average, higher signalling males are of higher quality (Johnstone & Grafen 1992). It is even possible for low-quality males to have the absolutely highest level of signalling (Kokko 1997), which can also lead to signalling equilibrium as long as female behaviours are constrained to a directional preference (Proulx 2001*a*).

Kokko's (1997) results were instrumental in demonstrating that previously unanticipated age-dependent patterns of male advertisement can evolve because signalling can still be reliable under such circumstances. Moreover, the form of the organism's life history (e.g. semelparity versus iteroparity) has a large influence on the extent to which signalling evolves. Thus, it is clear that we must take life history into account when trying to understand the evolution of male signalling. What is not clear from previous results, however, is how and why an organism's life history influences whether reliable signalling evolves. For example, there has been considerable effort devoted towards deriving explicit conditions under which reliable signalling will evolve when life-history considerations are ignored (i.e. the handicap criterion of Grafen (1990)). However, as yet there has been no attempt to define the handicap criterion when opportunities for future success are explicitly incorporated. Such results would be useful because they would tell us whether certain life histories are more conducive to the evolution of reliable signalling and, if so, why.

In this paper, we build a general analytical model of costly display in an iteroparous organism with senescence. We first consider the simplifying case of an organism that is constrained to choose its level of signalling at sexual maturity. The main result is that, whenever multiple reproductive bouts are possible, high-quality males reduce their allocation to signalling more than low-quality males, because their lifespan is more sensitive to changes in survivorship. This means that a display trait that meets the traditional definition of a handicap might not allow stable signalling. We then consider a case where males can adjust their level of signalling but have a fixed maximum lifespan. During the last reproductive episode, this model reduces to the semelparous case, but at earlier time points, high-quality males reduce their investment in display more than low-quality males. Thus, females who examine only older males as potential mates are more likely to mate with high-quality males because errors in perception will be less likely.

It has been suggested that females may prefer to mate with older males because old age is proof of high survivorship (Manning 1985). This idea is supported by the finding that males with higher survivorship are over-represented in samples of older males (Manning 1985; Kokko & Lindstrom 1996; Kokko 1998*a*), but has been challenged because males with high survivorship might have low overall fitness due to an inappropriate senescence schedule (Price & Hansen 1998; Brooks & Kemp 2001) and older males may have low-fertility sperm (Jones *et al.* 2000). An alternative argument is that older males are more honest signallers, so that even if older males do not have higher mean survivorship, females can get more information about the genotype of potential mates by restricting their attention to older males. In fact, the signalling game can cause current success to increase more steeply with investment in current reproduction, which can alter the senescence schedule so that more emphasis is placed on early survival.

2. A GENERAL LIFE-HISTORY MODEL WITH FIXED MALE DISPLAY

We first consider an organism in which males produce a display trait at sexual maturity and retain the trait throughout life. Males who are alive during a particular breeding season receive matings that depend only on their level of advertising (a) so that higher-quality males do not have an intrinsic 'fecundity' benefit (Getty 1998), i.e. among living males advertising at rate a, mating success does not depend on quality. We can then write male fitness as the product of the expected number of seasons spent breeding and mating success achieved by males who survive to breed.

$$w(q,a) = B(q,a)M(a), \tag{2.1}$$

where $B(q,a)$ is the expected number of breeding seasons and $M(a)$ is the mating success, which depends only on signal level. The optimality condition is that the total derivative of fitness with respect to advertising equals zero:

$$\frac{\partial B(q,a)}{\partial a}M(a) + B(q,a)\frac{\partial M(a)}{\partial a} = 0. \tag{2.2}$$

Note that this produces the relationship

$$\frac{B(q,a)}{\partial B(q,a)/\partial a} = \frac{-M(a)}{\partial M(a)/\partial a}. \tag{2.3}$$

A solution to equation (2.2) represents a fitness ridge on the advertising/quality fitness surface (Getty 1998). Signalling will be reliable when the ridge moves in the direction of higher signalling as quality increases. This means that, if we increase quality but keep advertising fixed, the sign of the left-hand side of equation (2.2) should become positive. In other words, a male who signals at the optimal level for a slightly lower-quality male will increase his fitness by increasing signalling. The optimal signalling function will be increasing in quality if

$$\frac{\partial^2 B(q,a)}{\partial a \partial q} M(a) + \frac{\partial B(q,a)}{\partial q} \frac{\partial M(a)}{\partial a} > 0, \tag{2.4}$$

as long as mating success depends only on signalling, so that $\partial M(a)/\partial q = 0$. Dividing through by the positive term $M(a)$ and substituting in the optimality relationship from equation (2.3), the condition becomes

$$\frac{\partial^2 B(q,a)}{\partial a \partial q} - \frac{(\partial B(q,a)/\partial q)(\partial B(q,a)/\partial a)}{B(q,a)} > 0, \tag{2.5}$$

which we will call the 'handicap criterion'. This resembles Getty's (1998) result when male success depends only on the signalling level and $B(q,a)$ is interpreted as the probability of surviving to a single breeding attempt. Grafen's (1990) result can similarly be recovered under the assumption that a male's perceived quality only depends on his signalling level. If we assume that there are discrete age classes, that juveniles have a fixed survivorship of s_j, that age-specific senescent mortality ($\mu(t)$) is a risk that is independent of quality or advertising, and that the yearly survivorship is $s(q,a)$, then we can write

$$B(q,a) = s_j \sum_{t=1}^{\infty} \left((1 - s(q,a)(1 - \mu_t)) \prod_{\tau=1}^{t} s(q,a)(1 - \mu_\tau) \right). \tag{2.6}$$

This is the expectation of the time of death, which we find by summing up the year of death (t) multiplied by the probability of dying in year t, multiplied by the probability of having survived all previous years (the product on the right). Although we require that the male advertising level is fixed for life by assumption, when signalling-independent mortality is constant ($\mu_t = \mu$), then adaptive male behaviour leads to a constant seasonal investment in advertising. Because the display is fixed, the costs of display are assumed to be due to bearing the trait, not producing it. The life-history model laid out in equation (2.6) is fairly general because it allows for senescent mortality to be any function of age and for a fixed maximum lifespan ($\mu_T = 1$). We assume that advertising has a negative effect on survivorship and, by definition, quality has a positive effect.

(a) *Semelparous species*

Most previous studies have modelled fitness as the product of survivorship and mating success. This either implies a semelparous organism or that survivorship is actually a lifetime measure of the number of breeding attempts. In our model for a semelparous organism, the probability of surviving to breed is the probability of surviving the juvenile period multiplied by the probability of surviving the advertisement-induced mortality,

$$B(q,a) = s_j s(q,a). \tag{2.7}$$

We can compute the handicap criterion by substituting this form into equation (2.5) to get

$$\frac{\partial^2 s(q,a)}{\partial a \partial q} - \frac{(\partial s(q,a)/\partial a)(\partial s(q,a)/\partial q)}{s(q,a)} > 0, \tag{2.8}$$

which is equivalent to the handicap criterion as derived by Grafen (1990). Note that, as pointed out by Getty (1998), this condition only needs to be met near the optimal advertising level. That is to say, this condition depends on the costs of altering signalling levels, not the total cost of signalling. However, if this criterion holds for all signalling levels, then a satisfying interpretation of equation (2.8) is that the proportional reduction in survivorship is greater for lower-quality males (see electronic Appendix A). Moreover, this interpretation is applicable directly to measurements of the costs of signalling when male signal is artificially manipulated, even when equation (2.8) only holds along the optimal advertising path. If the proportional reduction in survivorship is measured to be larger for low-quality males then the handicap criterion is met.

Another way of showing this is by considering a survivorship function, which has no interaction between quality and advertising. If the yearly survivorship function is

$$s(q,a) = f(q)g(a), \tag{2.9}$$

then survivorship consists of two independent trials; the male must survive both a quality-related risk and an advertising-related risk. When this function is substituted into the left-hand side of inequality (2.8), we find that it is zero. This implies that, for any fixed female mating preference function, all males will signal at the same level, regardless of quality. We will refer to this survivorship function as the 'no interaction' function. This function is useful because, if it produces a negative relationship in equation (2.5) for a particular life history, then we know that the handicap criterion has shifted. This suggests that when there is some interaction between quality and advertising, such that low-quality males have greater proportional reductions in yearly survivorship, it is possible that advertising will not be an increasing function of quality.

(b) *Iteroparous species without senescence*

In nature, many iteroparous species have rates of senescence that are difficult to detect and thus have lifespans that are determined primarily by their yearly age-independent mortality rate (Nisbet & Cam 2002). The expected time spent breeding is

$$B(q,a) = s_j s(q,a)/(1 - s(q,a)). \tag{2.10}$$

Males who have higher survival probabilities will have greater expected lifespans, and higher sensitivity of lifespan to survivorship, as can be shown by differentiating B with respect to s.

$$\frac{\partial B}{\partial s} = \frac{s_j}{(1 - s)^2}, \tag{2.11}$$

which increases as s approaches one. Inserting the expression for the expected time spent breeding into equation (2.5) yields

$$\frac{\partial^2 s(q,a)}{\partial a \partial q} s(q,a)(1 - s(q,a)) - \frac{\partial s(q,a)}{\partial a}\frac{\partial s(q,a)}{\partial q}(1 - 2s(q,a)) > 0. \tag{2.12}$$

For this life history, the traditional handicap criterion does not apply. Because the term $1 - 2s(q,a)$ can be either negative or positive, it is not sufficient that the proportional reduction in yearly mortality is greater for low-quality males for inequality (2.12) to hold true. This does not mean that no iteroparous species will evolve honest signalling, just that the requirements are more extreme.

We can insert the 'no interaction' survivorship function into the left-hand side of inequality (2.12) and obtain

$$\frac{f'(q)g'(a)}{(f(q)g(a) - 1)^2}, \tag{2.13}$$

which is negative because survivorship is assumed to increase in q but decrease in a. Thus, the 'no interaction' survivorship function produces decreasing display as a function of quality. What brings about this greater reduction in advertising by high-quality males is the fact that for high-quality males future success is more sensitive to a change in yearly survivorship. This is because a change in survivorship is compounded over more years, on average.

(c) *Iteroparous species with senescence*

First, we consider a life history where senescence is manifested by a maximum lifespan T, at which point the probability of living to the next season is zero ($\mu_T = 1; \mu_t = 0, \forall t < T$). The expected number of breeding seasons is

$$B(q,a) = s_j s(q,a)\frac{1 - s(q,a)^T}{1 - s(q,a)}. \tag{2.14}$$

Again, individuals with higher survivorships have higher expected breeding lifetimes and the sensitivity of B to survival probability is higher for high survivorship males,

$$\frac{\partial B}{\partial s} = s_j \frac{1 - s^T(1 + T(1 - s))}{(1 - s)^2}, \tag{2.15}$$

which is also increasing in s, as long as $T > 1$. The analytical solution for the handicap criterion of this life history is complicated, but we can again appeal to the 'no interaction' survivorship function. By substituting equations (2.14) and (2.9) into equation (2.5), we find that advertising is a decreasing function of quality. This shows that an infinite possible lifespan is not necessary to alter the handicap criterion; rather, any life history that includes multiple reproductive bouts requires a stronger condition.

3. AGE-DEPENDENT MALE DISPLAY

(a) *Signalling increases with age*

In the previous sections, we considered species that produce a fixed display that lasts throughout the life of the male. When senescence causes mortality rates to change with age, the optimal advertising schedule will typically be dependent on the age of the male. We can include these effects in a model with a fixed maximum lifespan to see if the results based on fixed displays are general. For simplicity, we assume that senescence is reflected by a maximum age of T, so that $\mu_T = 1$ but $0 < \mu_t < 1$ for $t < T$. We also assume that $\mu_t \leqslant \mu_{t+1}$ so that senescence causes mortality rates to increase with age. For $T > 1$, we can start by considering the optimal display of males who are alive at this maximum age. We can write the fitness of these males, conditioned on the fact that they are alive, as

$$w_n(q,a) = s(q,a)M(a), \tag{3.1}$$

which is the same fitness function as in the semelparous model. Thus, in the last time step, if $s(q,a)$ satisfies the handicap criterion, display amongst the oldest males will be an increasing function of quality. At any earlier age class, we can partition the fitness of a male into current and future success to get

$$w_t(q,a) = s(q,a)(M(a) + w_{t+1}(q)). \tag{3.2}$$

We can find the optimal signalling level by differentiating with respect to the advertising level in the current age class, realizing that this will not change the optimal advertising levels in the future, to get

$$\frac{\partial w_t(q,a)}{\partial a} = \frac{\partial s(q,a)}{\partial a}(M(a) + w_{t+1}(q)) + s(q,a)M'(a) = 0. \tag{3.3}$$

This equilibrium condition can be used to determine how advertising will change with male age. Just as female reproductive value is expected to decrease with age (under the life-history assumptions of this section) (Roff 1992), male reproductive value is expected to decrease with age (see electronic Appendix B), as well as increase in quality.

To determine how male advertising will change with age, we can ask how the derivative of fitness with respect to advertising changes with the residual reproductive value. For some age class t, we know that at equilibrium

$$\frac{\partial w_{t-1}(q,A^*)}{\partial a} = \frac{\partial s(q,A^*)}{\partial a}(M(A^*) + w_t(q)) + s(q,A^*)M'(A^*) = 0, \tag{3.4}$$

where A^* is the optimal advertising rate at age t. Because w_t is multiplied by a negative term ($\partial s(q,A^*)/\partial a$), we know that increasing w_t will make the advertising derivative of fitness negative and cause the optimal advertising level to decrease. Because w_t is larger for smaller t (see electronic Appendix B), the youngest reproductively active males should have the lowest displays. This occurs without an appeal to size constraints or investment in growth. This means that the difference between the signalling level of the highest-quality males and males who signal the least will be smallest among the youngest males.

(b) *The optimal signalling curve changes with age*

The previous section demonstrated that, in a species where quality-independent mortality rates are constant or increase with age, then signalling will increase and reproductive value will decrease with age. This means that, in some sense, signals of older males are more useful to females because they cover a broader range of signals and so will be more easy to distinguish. However, the ability of a female to distinguish between two males of different quality is likely to depend on the difference between their signals. One metric for this difference is the rate at which signalling changes as a function of quality, or the slope of the optimal signalling curve. If the optimal signalling curve becomes steeper as males age, then the absolute difference between the signals of two males of different qualities will increase with age. In this section, we ask how this slope changes when there is an opportunity for future reproduction.

Consider a species where a proportion of males experiences more than one breeding season. Fitness can be written as

$$w(q,a) = s(q,a)(M(a) + pw_r(q)), \tag{3.5}$$

where $w_r(q)$ is the residual reproductive value and can be thought of as only a function of q, and p is the probability of surviving between breeding seasons. The optimal signalling level is a solution to the equation

$$\frac{\partial s(q,a)}{\partial a}(M(a) + pw_r(q)) + s(q,a)\frac{\partial M(a)}{\partial a} = 0. \tag{3.6}$$

To find how signalling is affected by changes in the survival probability, we can implicitly differentiate equation (3.6) with respect to p to get

$$\frac{\partial A}{\partial p} = \frac{-(\partial s(q,a)/\partial a)w_r(q)}{C_2}, \tag{3.7}$$

where

$$C_2 = \frac{\partial^2 s(q,A^*)}{\partial a^2}(M(a) + pw_r(q)) + 2\frac{\partial s(q,A^*)}{\partial a}\frac{\partial M(A^*)}{\partial a} + s(q,A^*)\frac{\partial^2 M(A^*)}{\partial a^2}$$

is the second-order optimality condition. This term is negative because both $\partial s(q,a)/\partial a$ and C_2 are negative, so increasing opportunity for future success decreases current investment in advertising. Our suggestion is that the reduction in signalling due to the availability of future success will be larger for higher-quality males because they have more future success. However, we have not been able to find general conditions that prove this claim.

We can make some headway by appealing to the 'no interaction' survivorship function and find that, when $p \approx 0$, then

$$\frac{\partial^2 A}{\partial p \partial q} = \frac{-f'(q)f(q)g'(a)g(a)M(a)}{C_2}, \tag{3.8}$$

which must be negative at any equilibrium. Thus, for the 'no interaction' function, increasing opportunities for future success cause high-quality males to reduce signalling more than lower-quality males.

Of course, the 'no interaction' survivorship function is not realistic and was used only as a limiting case to show that high-quality males can reduce signalling more than lower-quality males. We took two complementary approaches to investigate this phenomena further: the first was to combine the analytical results from this section with the results from species without senescence; the second was to calculate the reduction in signalling for specific examples.

Because the last time step is just like the semelparous case, the traditional handicap criterion will determine whether display is increasing in quality. If we assume that signalling causes a larger proportional reduction in survivorship for lower-quality males, then in the last time step living males will display in a condition-dependent manner. If the maximum age is large, then the optimal age-dependent signalling function will be approximately given by the iteroparous model without senescence. When the survivorship function does not satisfy inequality (2.12), then signalling will be dishonest among young males but will be honest among older males. For such survivorship functions, higher-quality males will reduce signalling more than lower-quality males at the earliest age classes.

We can also get some general ideas about how gradual senescence will alter male signalling. In a senescing organism, residual fitness will always go down as a function of age, so that as individuals age, the benefit of delaying reproduction goes down. Older individuals will advertise in approximately the way that is expected based on a semelparous model. Thus, if the semelparous handicap criterion is met, then older individuals will advertise honestly. Younger individuals will have reduced investment in advertising due to an increase in the future component of fitness, but honesty will depend on how the difference in future success between high- and low-quality males changes as individuals age. If high- and low-quality males have greater differences in future reproduction when young than when old, then signalling will be less honest among young males. That is, even if signalling does not become negatively correlated with quality in young males, the differences in advertising between low- and high-quality males will be smaller. Females who examine younger males will have more difficulty discriminating between males of different quality.

To investigate how signalling is reduced in intermediate age classes, we have used several functional forms for survivorship and mating success. Figure 1 shows how male display changes for two sets of survivorship and mating success functions. In each example, the highest-quality males reduce signalling the most in earlier age classes. In figure 1*a*, we used a survivorship function and a mating success function with a negative second derivative, while the functions in figure 1*b* have positive second derivatives. We used functions with different shapes to determine if the shape of the function has a part in determining whether or not higher-quality males lower signalling more than lower-quality males. Each of these examples meets the semelparous handicap criterion, but not the iteroparous criterion. As predicted, signalling is reliable among older males, but not among younger males. At intermediate age classes, signalling can be reliable, but the differences in signalling between males of different quality are reduced.

We have also examined the reduction in signalling for every combination of survivorship and mating success function (listed in table 1). For all combinations that produce a signalling equilibrium, we find that higher-quality males reduce signalling more than lower-quality males.

4. DISCUSSION

The hypothesis that females prefer to mate with older males has mostly focused on how male quality is likely to change with age, and not on how male signalling might change with age (Manning 1985; Kokko & Lindstrom 1996; Price & Hansen 1998; Kokko 1998*a*; Beck & Powell 2000; Brooks & Kemp 2001). Our suggestion is that older males will provide better signals of quality to females, so

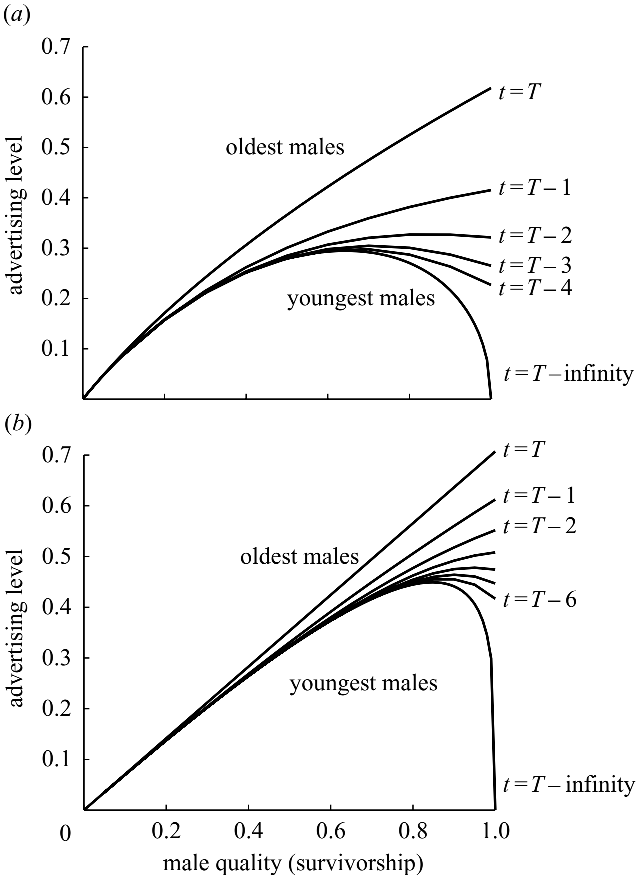

Figure 1. The reduction in signalling levels and reliability in an iteroparous species. In (*a*), the yearly survival function is $s(q,a) = qe^{-a/q}$ and the mating success function is $m(a) = a/(a+1)$. In (*b*), the survival function is $s(q,a) = q(1-(a/q)^2)$, and the mating success function is $m(a) = a^2$. The optimal signalling level in a semelparous species or among old males (highest curve) is always greater than for younger males. Each age curve represents a younger age group. The lowest curve is for a species with no maximum age class (or the limit as $t \rightarrow T - \infty$).

Table 1. Functional forms for survivorship and mating success.

survivorship	mating success
$qe^{-a/q}$	$a^2/(a^2+1)$
$q(1-(a/q)^2)$	$a/(a+1)$
q^a	a^2
$q(1-a)$	$e^a - 1$
$1/(1+a^2(2-q^2)^2)$	e^a

that females who mate exclusively with older males will benefit, even if the distribution of male quality does not differ between age classes. The change in male signalling can bring about the observed preference of females for older males (Sundberg & Dixon 1996; Richardson & Burke 1999; Dunn & Cockburn 1999) through either passive or active age-based female preferences. If females are able to measure male age directly then they might only consider older males as potential mates and express an active preference for male age. If male age cannot be directly determined, then females who prefer males with larger displays are still more likely to mate with older males.

In this paper, we have focused on age- and quality-specific patterns of male display under the assumption that females prefer males who advertise more, regardless of age. Our results show that, when the potential for future reproduction is taken into account, the traditional handicap criterion is not enough to guarantee that signalling increases with quality. This result applies to models both with and without senescence. When younger males do not signal reliably, but older males do (figure 1), then we can unambiguously state that older males provide more reliable information to females. However, we also show that, in some situations, the range of signals produced goes up with age, as does the slope of the advertising function, but males of all ages signal reliably. How shifts in signalling are translated into mating frequencies depends on female mating strategies and the ability of females to perceive differences in signals with different means.

Our results suggest that signalling will be most reliable among older age classes. While signalling in young males may be an increasing function of quality, it is likely to increase less quickly than in older males. Thus, a female who examines a young male may have more difficulty accurately inferring his quality than a female who examines an older male due to limitations in female perception (Proulx 2001*b*). Thus, even if mean male quality does not increase with age, females who choose older males are likely to mate with high-quality males. This effect will be tempered by the amount of time that females can reasonably spend choosing mates and by reductions in male fertility with age (Jones *et al.* 2000; Mack *et al.* 2000).

In several species, some male traits reveal age but not quality, whereas other traits are condition related (Yezerinac & Weatherhead 1997; Part & Qvarnstrom 1997). For instance, male collared flycatchers have a wing band that increases in size with age and a forehead patch that responds to manipulations that are designed to alter condition (Gustafsson *et al.* 1995). While females would benefit by preferentially mating with older males even if the frequencies of low- and high-quality males were the same for all ages, this benefit would be larger if the frequency of high-quality males increased in older age classes. When females have both direct information on male age and information on male quality, then we would expect male mating success to be influenced by both male age and signal, and we would even expect an interaction between age and signal.

Even if mechanisms to infer male age independently do not exist, adaptive female choice can result in a preference for older males. Our results suggest that, as long as the residual fitness of males decreases with age, then advertising will be greater among older males. Thus, a simple preference for a large signal will result in a preference for older males who produce reliable signals. Under this scenario, we would expect that the male signal will determine mating success, but that age corrected for signal strength would not.

If the age-specific changes in the reliability of signalling characterize male display, then we would expect to see: male display increase with age; female preference for older males; and females to be more choosy when mating with younger males. There is some support for the first two predictions, although increases in male signalling with age are sometimes excluded from analyses as confounding factors (Part & Qvarnstrom 1997). For example, song characteristics change with age in the willow warbler, as shown by a study that tracked individuals through time (Gil *et al.* 2001). This study isolated the effects of differential mortality and age-specific signalling by following individual males as they aged and by analysing cross-sectional data within a single year. Although some of the same song characteristics were found to differ between age classes through the cross-sectional approach and between years in the longitudinal approach, other characteristics did not (Gil *et al.* 2001). This points out the importance of studies that track individual life-history trajectories and avoid the confounding effects of differential mortality. The prediction that female choosiness depends on male change is more equivocal. A recent study of fairy wrens found that male moult date was a significant factor in determining male mating success and is presumed to be correlated with display in some way (Dunn & Cockburn 1999). The authors found that moult date was correlated with age, in agreement with our predictions. They also found that moult date alone explained much of the variance in mating success and that age and moult date together did not explain more variance. This suggests that, in fairy wrens, females do not have direct access to information on male age.

Stable signalling between males and females requires that the female preferences for male signals enforce a male signalling strategy that in turn makes mate choice beneficial to females. We assumed that males benefited by increasing their level of advertising, rather than attempting to find a signalling equilibrium for both males and females. However, as long as increases in female preference for large signals increase female fitness, then our results will hold. This occurs if the utility that females derive from males has a positive relationship with male survivorship (Proulx 2001*a*).

The primary utility that females derive from males may be parental care. Because male parental care typically comes after mating, it may be difficult to enforce honest signalling (but see Viljugrein 1997). However, when male survivorship saturates with energy reserves and the opportunities for extra-pair copulations are low, then male parental care patterns are likely to follow male advertisement patterns (Kokko 1998*b*). This suggests that, whatever pattern of advertising is induced by survivorship trade offs, the same pattern of parental care will be optimal. Thus, even if high-quality males signal less because they place more weight on future success, females will prefer males with large signals because they place more weight on all components of current success, including parental care. Conversely, if females receive only genetic benefits from males, then there may be no signalling equilibrium if high-quality males signal at lower levels than low-quality males.

When females receive only genetic benefits and the attractiveness of sons is determined in a condition-dependent manner, then the age-independent survivorship of males represents the currency of utility. If the expected utility of a male to a female is an increasing function of display, then it is widely held that female preferences can be maintained (Grafen 1990; Johnstone & Grafen 1992; Kokko 1997; Proulx 2001*a*). This was the case in Kokko's (1997) study, where even though some low-quality males signalled at high levels, they were at low enough frequency such that signalling and quality were always positively correlated. Our model, which differs from Kokko's (1997) in that we do not restrict our attention to a single cost function, shows that signalling can be dishonest among young males, which are the most common age class. Thus, it is possible for utility to decrease with signal over some range. Even when signalling is honest within every age class, quality is likely to be a non-monotonic function of signal because of the transitions between age classes (figure 2). However, signalling amongst old males is predicted to be honest (as long as the standard handicap criterion holds) and to be greater than in younger males. Thus, even though quality might decrease with signal over some range, it will eventually increase so that signalling will be honest for the males that signal the most. This situation was investigated by Proulx (2001*a*) and can lead to a stable signalling equilibrium as long as female behaviours are constrained to express a relative preference.

Recent empirical work on sticklebacks has shown that male display can be non-monotonically related to male quality (Candolin 1999, 2000). Previous work using models that include growth dynamics suggests that low-quality males might make a large investment in advertising at the end of life, while high-quality males invest more in advertising at earlier ages (Kokko 1998*a*; Candolin 1999). By contrast, our results can explain reversed signalling patterns without growth dynamics, and suggest that this reversed pattern should be most extreme early in life, as observed by Candolin (2000).

We adopted the simplifying assumption that the quality of an individual is constant and does not depend on past actions. This is unlikely to be true in nature, as investment in display traits is likely to take resources that could be devoted to growth, fat reserves or maintaining soma (Rowe & Houle 1996; Abrams & Ludwig 1995). It is more difficult to determine the optimal advertising strategy in a model with growth, but some results do exist (Kokko 1997). Kokko (1997) developed a model of male display that includes growth (carry-over of quality) and a model of trait development that can reflect long-term or short-term traits (carry-over of trait). Her model included a specific functional form for survivorship that was strong enough to guarantee honest signalling in a long-lived species, two discrete classes of males, and focused on cases with growth or trait carry-over. These details confound a direct comparison with the present study.

We have shown that, in a life history with senescence, the traditional semelparous handicap condition will exactly apply only at the end of the lifespan, when death is imminent. Because individuals with higher survivorships typically have greater future reproductive success, their optimal strategy is to reduce their investment into current reproduction more than low-survivorship individuals. This applies equally to any component of current success, male or female, and includes investment in male display. Even if senescence causes a gradual increase in the advertising-independent mortality rate, the conditions for honest signalling are more stringent. Only when age-dependent (but quality-independent) mortality decreases with age can residual reproductive success increase with age, violating our assumptions. Thus, in the rare instance

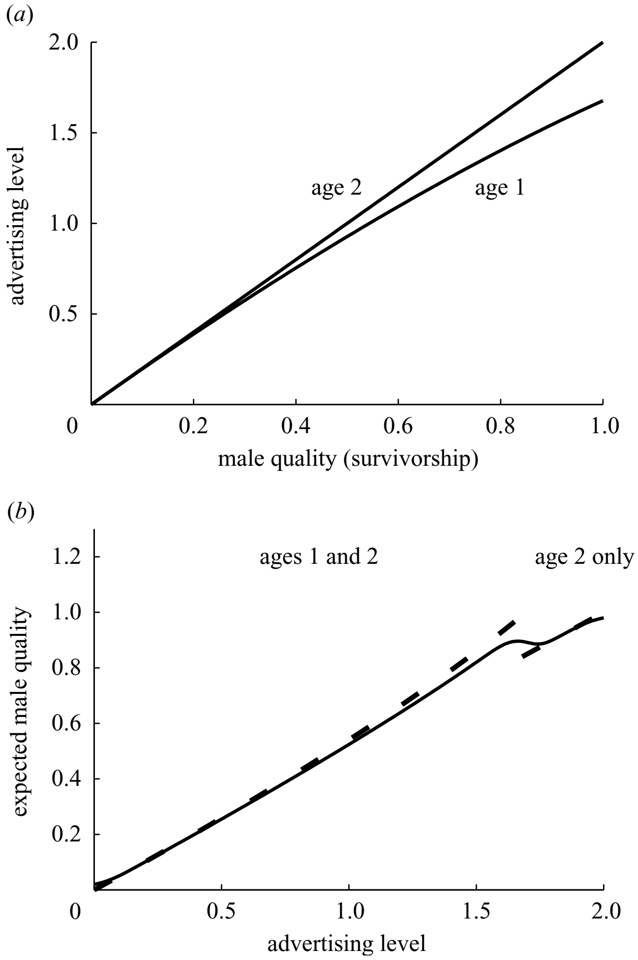

Figure 2. (*a*) The optimal advertising levels for males of two ages. In this example, mating success of males is defined as $M(a) = a^2$ and survivorship is defined as $s(q,a) = qe^{-a/q}$. The optimal male advertising strategy is first found for age 2, which is assumed to be the maximum age. Then, the advertising strategy for age 1 is found by maximizing $s(q,a_1)(M(a_1) + s(q,a_2)M(a_2))$, where a_2 has already been found. Advertising increases with age in both age classes, but increases faster at age 2. (*b*) The expected quality as a function of male advertising level. The dashed line shows the expected male quality when there is no female perceptual error. Male quality is assumed to be uniformly distributed. Because the advertising levels of males in age 1 overlap with males of age 2 the quality of a male cannot be unambiguously inferred. Below an advertising level of about 1.5, both males signal, and expected quality increases with age. Only 2-year-old males signal above about 1.5, causing a sudden drop in expected male quality followed by an increase. Females who have a preference for a high-quality signal will still mate with higher-quality males than if they were to mate at random. The solid line shows the expected quality of a mate as a function of the observed advertising level when perceptual error causes observed male signal to be normally distributed with variance of 0.05 around the actual signal.

where mortality rapidly decreases with age, the handicap condition might be relaxed. Our results apply exactly to a limited set of conditions, and more work is needed in this area, but they shed light on the factors that can alter the requirements for honest signalling.

We are not suggesting that honest signalling will not evolve in long-lived species, but rather that the interaction between quality and signal on survivorship must be stronger than was previously believed in order to explain the widespread evidence of condition-dependent signalling. Because male display is widespread, this suggests that the signalling costs steeply decrease with male quality. Our results suggest that male display will also be an increasing function of age, even after growth has stopped. As males age, differences in signalling between quality classes are predicted to increase, making female choice more effective among older males. Thus, female preference for old males is predicted even when older males are not, on average, of higher quality than younger males.

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