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Costs of mate advertisement

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ABSTRACT. *Costs of mate advertisement.*- Mate advertisement should be thought of and subjected to similar trade-offs as other life-history traits. Sexual displays should therefore be individually optimised and the level of display can depend on both male quality and environmental harshness. Field studies of the costs of male displays have revealed a number of mechanisms that may generate a cost of reproduction (defined as negative effects on future reproduction). Costs can be in terms of increased predation, parasitism or disease. Costs can also be generated by the display being energetically demanding that may affect individual somatic maintenance. However, because of individual optimisation, intra specific observational studies do not always reveal a cost of reproduction. Experimental manipulation of male displays in swallows has revealed increased mortality when male tails were elongated. Also, inter specific comparisons suggests that in species subjected to intense sexual selection, males have higher mortality rates than females.

KEY WORDS. Life-history evolution, Sexual selection, Display, Trade-off, Cost of reproduction

Introduction

In studies of the evolution of life-history traits it has long been recognised that, because of resource limitation, allocation of resources to one trait can only be made at the expense of another, individuals therefore often face-trade offs (Williams, 1966; Bell & Koufopanou, 1986; Lessels, 1991). Stearns (1992) listed 45 possible trade-offs between 10 different life-history traits. Five of these trade-offs have also received considerable empirical consideration (current reproduction vs. survival; current vs. future reproduction; current reproduction vs. parental growth; current reproduction vs. parental condition; and number vs. size of offspring).

By contrast, studies of sexual selection have commonly focused only on the advantage of the investment in mate advertisement (Harvey & Bradbury, 1991). To date it is a commonly held view that larger sexual ornaments, increased song out-put and brighter coloration in males exists because increased display entails a mating advantage. In this paper any morphological, physiological or behavioural adaptations that serve to attract females, i.e. mate advertisement, will be referred to as a display. However, fewer studies have examined the costs of mate advertisement. Therefore, the trade-off between sexual displays and reduced survival is almost unknown in any species. Since mate advertisement commonly makes up a large fraction of male reproductive effort, theories about optimal male investment in mate advertisement ought to follow the same principles as for any life-history trait.

A model of optimal investment

Nur and Hasson (1984) modelled how males should invest in mate advertisement given that increasing signalling levels confer a mating advantage but also reduce survival. Let F stand for mating success and S for survival, optimal trait values (x) are found where the reproductive value ($V(x)=F(x)*S(x)$) is maximised. In Figure 1, S(x) is modelled as a monotonically decreasing function with three different slopes: with steeper slopes, survival decreases faster with increasing x. The three slopes of S (S_0, S_1 and S_2) can be thought of as either different kinds of males with different susceptibilities (male quality) or an environmental gradient that increases in harshness from 0 to 2. In the latter view, the optimal mate advertisement levels (x_0, x_1 and x_2) could be seen as male reaction norms to the environment (see Stearns, 1991 and Thompson, 1991 for discussions of reaction norms).

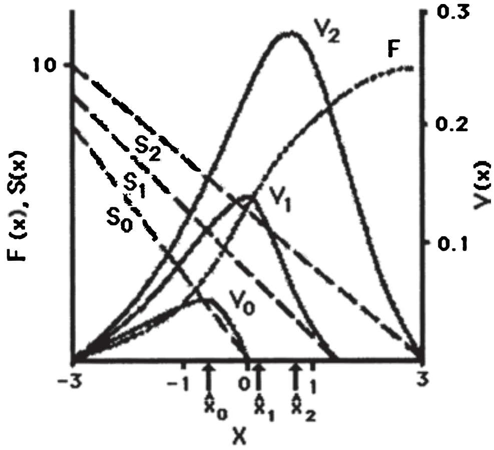

FIGURE 1. Nur and Hasson's (1984) multiplicative model of optimal male advertisement. The model assume three classes ("conditions") of individuals. S describe survival, F the mating advantage and V fitness (F multiplied by S) and x is the level of advertisement. Each class of males (0, 1 and 2) obeys its own S-curve and generates its own V-curve. x_0, x_1 and x_2 that maximize the respective V-values. (After Nur & Hasson, 1984).

[Modelo multiplicativo de Nur y Hasson (1984) de señalización óptima del macho.]

Indirect evidence for effects of male quality on the level of sexual displays comes from studies of an often observed age dependence on the expression of secondary sexual characters. Furthermore, diseased individuals often show reduced levels of mate advertisement. For example, yearling male black grouse (*Tetrao tetrix*) have shorter tail ornaments as compared to older (fig. 2a). In fallow deer (*Cervus dama*), male antlers increase in size up to the their fifth or sixth year of life (Chaplin & White, 1969). Male black grouse heavily infected with a range of gut parasites grew shorter tails less parasitised (fig. 2b) and males with high loads of microfilaria produced by a nematode worm had shorter tails independent of the effect of age (fig. 2c).

Indirect evidence for the existence of reaction norms on male display levels comes from adjustments of display and courtship levels with increasing predation pressure. In male guppies (*Poecilia reticulata*), populations differ in the mean intensity of male coloration and this variation has been shown to covary both with light conditions and predation pressure (Endler, 1980, 1983, 1992; Magurran & Seghers, 1990). Males living under more severe predation regimes tend to be more drab.

Field studies

The theoretical trade-off between mate advertisement and survival can be generated by a

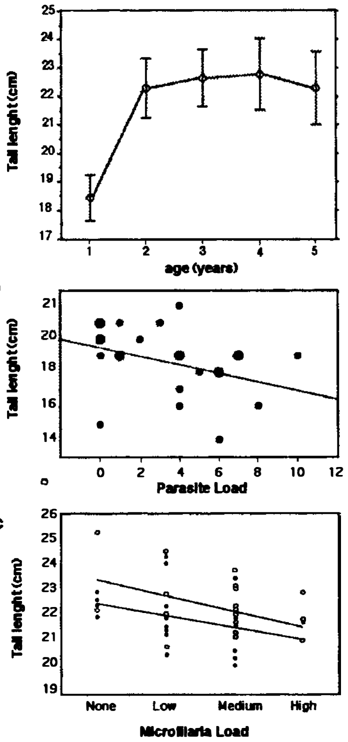

FIGURE. 2. a. Tail length in relation to age in male black grouse. Vertical bars indicate ±1 S.D (ANOVA, $F_{4,160}=124.3$, $P<0.0001$). b. The relationship between length of the ornamental tail feathers of black grouse (*Tetrao tetrix*) and intestinal parasite load ($y=19.6-0.24x$, $r^2=0.27$, $P<0.004$). Parasite load was calculated as follows. Seven types of parasites were found by Lund (1954) in birds shot in Norway and the intensity of each was given as absent, low or high. Abscence was given the score 0, low 1 and high 2, the index is the sum of these scores for each bird (from Höglund et al., 1992). c. The relationship between length of the tail feathers and microfilaria load of male black grouse. Open symbols and the upper line represent males 3 years or older, filled symbols and the lower line represent 2-year-old males. There was no diference in slopes (ANCOVA $F_{1,45}=2.28$, $P=0.14$) but the adjusted means differ ($F_{1,3}=6.23$, $P=0.02$)(from Höglund et al., 1992).

[Relación entre la longitud de la cola de machos de *T. tetrix* y: a. la edad en años; b. cantidad de parásitos intestinales; y c. cantidad de microfilaria.]

number of mechanisms in wild animals. Increased displays can lead to increased attraction of predators, parasites and diseases. Furthermore, individuals can use up the resources needed for metabolic maintenance and therefore freeze or starve to death.

Burk (1982) reviewed the evidence of predation on sexually signalling males in insects. The cases where an attempt to quantify the costs of display have been made are included in table I. For example, male field crickets (*Gryllus integer*) call to attract females. However, calling males do not only enjoy a mating advantage of calling but also suffer from parasitism from a tachinid fly that use male calls to phonotactically orientate towards calling males (Cade, 1975, 1979; Cade & Wyatt, 1984). A similar argument has also been made for a vertebrate species, the túngara frog (*Physalaemus pustulosus*). In this species males call to attract females but bats, opossums and other frog species use the male calls to locate their prey (Ryan et al., 1981, 1982, 1983; Ryan, 1985).

In túngara frogs, predation is not the only cost on displaying males. Another possibility is that the energetically demanding calling behaviour may limit displays (Bucher et al., 1982; Ryan, 1985). Energetic cost of mate advertisement has been assessed in a few other vertebrate species (table I). For example, in two species of lek breeding birds, it seems as if male displays are checked by being energetically costly. In sage grouse (*Centrocercus urophasianus*) males who showed high levels of display (struts/day) also used more energy (Vehrencamp et al., 1989; fig. 3a). In great snipe (*Gallinago media*) males with low display rates had a median daily energy expenditure of about 250 kJ/day whereas males with high display rates had a median of about 425 kJ/day (fig. 3b; Höglund et al., 1992). In both these species there are reasons to believe that high display rates confer a mating advantage (Gibson et al., 1991; Höglund & Lundberg, 1987; Höglund et al., 1990).

Large energy expenditures do not necessarily generate a cost of reproduction. For this to be, large energetic costs need to affect future reproduction negatively. Since individuals are expected to optimise their own display levels, an effect on survival or future reproduction is not expected in observational field studies. However, if high display rates confer a mating advantage and displays beyond individual optima do not affect future reproduction, why do not all males display at maximum rates? In the case of great snipe, male metabolic intensity was on average 3.4 x the basal metabolic rate (BMR) for a wader of a mean body mass of 156.3 g (Höglund et al., 1992). This figure should be contrasted with the estimated daily existence energy requirement of non-moulting and non-reproducing birds which is 2.6xBMR and the suggested maximum sustainable work rate for birds which is 4xBMR (Drent & Daan, 1980). Thus the display behaviour of great snipe males keeps them at a metabolic rate close to the maximum that they can sustain. If there are differences in male condition it is plausible that the variation in male display performance can be explained by individual quality differences and that males optimise their display rates to what they can afford.

Great snipe males burn energy when they display and as a consequence they loose body mass. During

TABLE I. Field studies in which mechanisms that may generate a cost of reproduction on displaying males have been investigated.

[Estudios de campo en los que se han investigado los mecanismos que pueden generar un costo de reproducción sobre los machos que realizan el comportamiento.]

Mechanism	Species	Reference
Display energetically demanding	*Hyla versicolor*	Wells and Taigen, 1986; Klump & Gerhardt, 1987
	Physalaemus pustulosus	Bucher et al., 1982
	Centrocercus urophasianus	Vehrencamp et al., 1989
	Gallinago media	Höglund et al., 1992
Display attracts predators and/or parasites	*Gryllus integer*	Cade, 1975; 1979
	Gryllodes supplicans	Sakaluk & Belwood, 1984
	Okanagana rumorsa	Soper et al., 1976
	Gasterosteus aculeatus	Moodie, 1972; McPhail, 1969; Semler, 1971
	Cichlasoma citrinellum	Barlow, 1976; Barlow & Ballin, 1976; McKaye & Barlow, 1976
	Poecilia reticulata	Endler, 1980
	Nothobranchius guntheri	Haas, 1976 a, b
	Physalaemus pustulosus	see Ryan, 1985

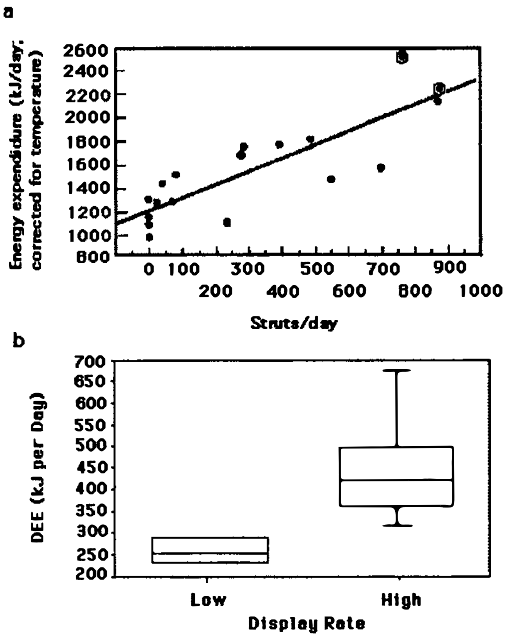

FIGURE 3. Energy expenditure in relation to strut rate in sage grouse (adjusted for effects of daily temperature variations). Circled points indicate two known successful mating males (y=1206.3+1.11x, r2=0.70, P=0.0001). (From Vehrencamp et al., 1989). b. A Tukey box plot (Feldman et al., 1987) showing the median daily energy expenditure (DEE) for great snipe males with low (n=4) and high (n=5) display rates. The cut-off point was choosen at ≥3.00 displays per minute. (From Höglund et al., 1992).

[Gasto de energía con respecto a la relaci6n al pavoneo en *Centrocercus urophasianus* (ajustados los efectos de las variaciones diarias de temperatura).]

a night of display activity for these nocturnal birds, males are estimated to loose on average 1.77 g body mass per h. Some of the body mass loss seems to be able to be compensated for when the birds feed. However, in May which is the early face of the lekking period for these birds, males lost on average 9 g (6% of the body mass) over an 11 day period. Later in the season no further mass loss was observed (Höglund et al., 1992).

As mentioned above, it is not always possible to show a cost of reproduction in intra-specific studies. Rather, the opposite pattern could be expected: males who show high levels of mate advertisement and consequently high mating success could be the males in the best condition. If so, such males can also show the best survival. An example of this pattern is the black grouse in which the most successful males had higher survival when compared to less successful males (Alatalo et al., 1991). One way around this could be to experimentally adjust individual male display levels beyond the level originally expressed by the males themselves. In swallows (*Hirundo rustica*) males in which tail length was experimentally elongated showed reduced survival compared to males in which tails were shortened or left as controls (Møller & de Lope unpubl. Ms).

Comparative studies

Not all natural populations are amenable to experimental manipulation. Inter-specific comparisons could, however, help to reveal costs of sexual selection. If mate advertisement is costly, males in sexually dimorphic species should show higher mortality rates than females of the same species. Thus we expect male biased mortality rates to be correlated with sexual dimorphism. To date, two such comparisons, one on birds and one on mammals, have been published (Promislow, 1992; Promislow et al., 1992).

In mammals, species in which males are larger than females show a male biased mortality indicating that in sexually selected species males pay a cost of sexual selection. However, in inter specific comparisons the effects of shared ancestry need to be controlled for otherwise similarities between closely related taxa may lead to correlations that are unrelated to the question under investigation (see Harvey & Pagel, 1991; Brooks & McLennan, 1991). Rather than using the actual values for each species, a method of removing the effects of shared ancestry is to use the differences between closely related taxa as independent observations. When such a contrast analysis (Pagel, 1992) was performed there was still a correlation between dimorphism and male biased mortality, suggesting that the relationship is not due to the effects of shared ancestry.

A similar pattern was revealed when the data from 28 North American passerines were used: there was a correlation between male biased mortality and male biased size dimorphism and increasing male plumage brightness. Thus the data from both mammals and North American passerines suggest that males in species subjected to intense sexual selection pay a cost of reproduction.

In summary, mate advertisement, like any other life-history trait, is subjected to individual optimisation. A number of mechanisms may generate a cost of reproduction on displaying males. Such mechanisms include attraction of predators, parasitoids and physiological exhaustion. To show that such mechanisms lead to a cost of reproduction, comparative studies or experiments are needed. In understanding how sexual displays evolve it is necessary not only to study the benefits but also the costs.

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Resumen

Costos de señalización del apareamiento.

La señalización de apareamiento debería ser tenida en cuenta y estar sujeta a compromisos similares a otros otros rasgos de los ciclos vitales. Las exhibiciones sexuales deberían, por tanto, ser optimizadas individualmente, y el nivel de exhibición puede depender tanto de la calidad del macho como de la severidad del nedio. Los estudios de campo de los costos de las exhibiciones del macho han revelado un número de mecanismos que pueden generar un costo de reproducción (definido como efectos negativos sobre la reproducción futura). Los costos pueden ser en términos de aumento de depredación, parasitismo o enfermedad. Los costos pueden ser generados también por la demanda energética de la exhibición que puede afectar al mantenimiento somático del individuo. Sin embargo, debido a la optimización individual, los estudios observacionales intraespecíficos no siempre revelan un costo de reproducción. La manipulación experimental de la exhibición del macho en golondrinas ha revelado un incremento de la mortalidad cuando se alargaron las colas de los machos. También, las comparaciones interespecíficas sugieren que en especies sujetas a una selección sexual intensa, los machos tienen tasass de mortalidad superiores a las hembras.

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