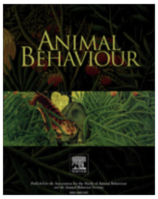
Animal Behaviour 84 (2012) 67–76

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Is there an expected relationship between parental expenditure and sex ratio of litters or broods?

Juan Carranza [a,b,*], Vicente Polo [c]

[a] Biology and Ethology Unit, University of Extremadura, Cáceres, Spain
[b] Ungulate Research Group, CRCP, University of Córdoba, Córdoba, Spain
[c] Departamento de Biología y Geología del Área de Biodiversidad y Conservación, Escuela Superior de Ciencias Experimentales y Tecnología (ESCET), Universidad Rey Juan Carlos, Madrid, Spain

ARTICLE INFO

Article history:
Received 3 October 2011
Initial acceptance 1 November 2011
Final acceptance 15 March 2012
Available online 16 May 2012
MS. number: 11-00782R

Keywords:
brood/litter size
offspring sex
parental care
parental investment
primary sex ratio
Trivers–Willard hypothesis

Parents may be selected to adjust the sex ratio of their offspring when parental expenditure yields different fitness returns from sons and daughters. This prediction is clear when parents produce only one offspring per reproductive attempt, but more complicated when parental resources are shared by several offspring, and parents may potentially influence the resource allocation among offspring as well as their number and sex. Here we present an optimization model to make predictions on how total parental expenditure may relate to the number and sex of offspring at every rank position within the litter or brood as well as the sex ratio of the litter/brood for the case of a large population with stable Fisherian sex ratio. We show that selection for sex ratio adjustment should be stronger for offspring at higher-ranking positions, for which the amount of resources received can be more predictable. Also, the relationship between parental resources devoted to a litter/brood of a given size and the primary sex ratio (proportion of males) is not expected to be a monotonically increasing function but rather a J-shaped relationship, steeper for small litters/broods and more extreme sexual dimorphism. Parental expenditure relates to increased sex ratio only for small variations in parental expenditure and for a given brood/litter size. For variable litter/brood sizes, a general relationship between parental resources and litter/brood sex ratio is not expected, although in practice pooling litters or broods of different sizes may produce negative relationships between parental expenditure and sex ratio of the litter/brood.

Trivers & Willard (1973) proposed that in species in which the relationship between parental resource allocation and fitness return differs for sons and daughters, the allocation of resources to offspring should adaptively relate to the sex of offspring. In particular, Trivers & Willard (TW) proposed that mothers in good condition should invest more in the production of offspring of the sex with higher reproductive return, usually males. The TW idea has been tested many times in a wide variety of species. However, the results are equivocal, and there is little consensus on whether the prediction is generally fulfilled or not (see Oddie 1998; Nager et al. 1999; Hardy 2002; Ewen et al. 2004; Rosivall 2008 and references herein). The TW hypothesis was based on three assumptions: (1) mothers in good condition can produce young of better condition, (2) condition of young at independence is translated into adulthood, and (3) male fitness will gain comparatively more than female fitness by slight advantages in condition. In addition to the problems related to the mechanisms involved (Krackov 1995; Mittwoch 1996; West & Sheldon 2002; Alonso-Alvarez 2006), another main unsolved problem is that the initial hypothesis outlined by TW was based on species that produce only one offspring per breeding attempt. Hence, in these species, the resources available to the offspring are directly related to the total amount of maternal resources, in agreement with assumption (1). However, it is unclear how to translate the predictions of the TW hypothesis to the many cases when several offspring share parental resources. In species that produce several offspring per reproductive attempt, parental resources must be divided among brood/littermates. In those cases, the share of resources obtained by any individual offspring will depend not only on total parental resources but also on the number and sex of siblings and the interactions between them (Kalmbach et al. 2005; Uller 2006; Nicolaus et al. 2009). In fact, many studies have shown asymmetries among litter/broodmates related, for instance, to birth weight or hatching order (e.g. Price & Ydenberg 1995; Mock & Parker 1997; Fernández-Llario et al. 1999; Smith et al. 2005). As a consequence, condition (1) of the TW hypothesis may not be fulfilled for all

---

* Correspondence: J. Carranza, Ungulate Research Group, CRCP, University of Córdoba, Campus de Rabanales, 14071 Córdoba, Spain.
E-mail address: jcarranza@uco.es (J. Carranza).

0003-3472/$38.00 © 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2012.04.007

offspring and it is not clear whether we should predict that mothers in good condition should bias the sex ratio of their progeny to produce more sons.

Only two models have so far addressed this issue: Williams (1979) and Carranza (2004). Williams (1979) suggested that the amount of parental resources invested in the brood should be related to a combination of the demands of brood size and offspring sex within the brood, leading to no correlation between parental resources and brood sex ratio. Williams's model dealt with the total number of male and female offspring in the brood but did not consider possible asymmetries among same-sex offspring in the amount of resources received, for instance related to birth weight or hatching order.

Carranza (2004) proposed a graphical model to derive predictions for sex adjustment when several offspring share limited parental resources. The central argument is that siblings within a brood compete for parental resources, either directly or indirectly, which influences the distribution of resources among them. Siblings within the brood may obtain different amounts of parental resources owing to initial asymmetries caused by parental strategies, such as hatching asynchrony, or differences in body mass and sex at birth, which might induce differences in competitive abilities between individual offspring. In these conditions, the optimal sex of the siblings might be arranged in a hierarchical order on the basis of their expected share of parental resources. As a consequence, hierarchical arrangement of the sexes within the brood, rather than variations in sex ratio of the whole brood, should be predicted (Carranza 2004).

In addition to differences in the mean share of parental resources, positions within the brood may also be characterized by variances in the expected share of parental resources (Carranza 2004). The reason for different variances rests on the combination of sibling competition and stochastic environmental effects. High-ranking siblings may have preferential access to limited parental resources, so that uncertainty in the amount of resources obtained should increase and be more dependent on environmental conditions, down the ranking of positions within the brood.

Differences in position-specific variances in resource share, and hence in fitness return, should have profound implications for selection for sex adjustment. One main implication is that benefits of parental expenditure on low-ranking offspring may not be realized owing to their relatively higher mortality (Carranza 2004). But another consequence, not included in Carranza's model, is that for any mean amount of expected resources received by an individual offspring, the benefits for parents of adjusting its sex will also depend on the confidence about whether the actual amount of resources finally received by the offspring will be within the range for which producing the chosen sex is better than producing the opposite sex. On the other hand, Carranza's model dealt with sex adjustment at positions within the brood but did not derive any prediction for either brood sex ratio or for the optimal number of offspring within the brood, mainly because of the graphical nature of the model.

Here we include all of these new effects in an optimization model. We include the variance in the expected resource sharing and the expected benefits associated with producing the right sex at every position within the litter or brood, and present a formal, quantitative model based on the framework previously proposed by Carranza (2004). Our main goal is to investigate the predictions that can be derived for the expected variation in number of offspring and litter/brood sex ratio as a function of the amount of parental resources allocated to the litter/brood, as first addressed by Williams (1979). We assume that breeders have to choose between the following strategies in relation to eventual increases in the amount of parental expenditure: (1) to adjust the sex of offspring at every position within the brood as proposed by Carranza (2004), taking into account the conditions at every position in the sense of the TW hypothesis, and as a consequence produce a bias in the sex ratio of the litter/brood; (2) to increase the number of offspring; or (3) a combination of both. Thus, our model investigates the optimal decision of parents in response to increases in total parental expenditure.

THE MODEL

General Description, Assumptions and Limitations

Optimal parental investment per offspring

We were interested in individual decisions on the number and sex of offspring within a litter or brood under constant population conditions, rather than in the problem of the evolutionarily stable strategy of sex ratio adjustment relative to the equilibrium at the population level. Thus, to simplify the problem, we consider the case of a large and stable population in which the sex ratio is already at the Fisherian equilibrium and individual decisions have negligible effects on the population sex ratio. Based on this simplification, we can remove population parameters on the expected individual fitness returns and limit the problem to the optimization of parental allocation of resources to one or other sex within the brood.

Consider a case where the fitness return for an individual breeder (e.g. mother) who invests in only one male or female offspring follows a positive sigmoidal-type function (e.g. Smith & Fretwell 1974; Lloyd 1987) of the amount of parental expenditure, r, devoted to this offspring. In the case of dimorphic species male, $\mu(r)$, and female, $\varphi(r)$, fitness returns are different functions of parental expenditure (Fig. 1a):

$$\mu(r) = a_\mathrm{m}\left[1 - \frac{1}{cosh[b_\mathrm{m}(r - r_\mathrm{m})]}\right], \text{ when } r \geq r_m \tag{1}$$

$$\phi(r) = a_\mathrm{f}\left[1 - \frac{1}{cosh\left[b_\mathrm{f}\left(r - r_f\right)\right]}\right], \text{ when } r \geq r_f \tag{2}$$

$\cosh(x) = 1/2(e^x + e^{-x})$ being the hyperbolic cosine function. Parameters a_m and a_f ($a_\mathrm{m} > a_\mathrm{f}$ in the case of polygynous, dimorphic species with males bigger than females) represent the asymptotic value of fitness return for sons and daughters (i.e. sex-specific fitness return for infinite parental expenditure). Parameters b_m and b_f are positively related to the magnitude of change in male and female fitness return, respectively, as parental expenditure changes. Finally, parameters r_m and r_f are the minimum amount of parental expenditures that a male or female offspring need to survive. That is, functions (1) and (2) reach zero values when $r < r_\mathrm{m}$ and $r < r_\mathrm{f}$, respectively (see Fig. 1a).

Since offspring size should trade with offspring number (Lack 1947; Smith & Fretwell 1974; Lloyd 1987), we assume that parents should maximize not fitness return per individual offspring but the rate of fitness return per unit of parental expenditure (Fig. 1b) when producing a son, $\mu(r)/r$, or a daughter, $\varphi(r)/r$.

$$\frac{\mu(r)}{r} = \frac{a_\mathrm{m}}{r}\left[1 - \frac{1}{\cosh[b_\mathrm{m}(r - r_\mathrm{m})]}\right], \text{ when } r \geq r_m \tag{3}$$

$$\frac{\phi(r)}{r} = \frac{a_\mathrm{f}}{r}\left[1 - \frac{1}{cosh\left[b_\mathrm{f}\left(r - r_\mathrm{f}\right)\right]}\right], \text{ when } r \geq r_f \tag{4}$$

Again, functions (3) and (4) reach zero values when $r < r_\mathrm{m}$ and $r < r_\mathrm{f}$, respectively (see Fig. 1b). Fitness return per unit of parental expenditure is maximized when parents allocate m^* and f^* units per individual sons and daughters, respectively (Fig. 1b). At the