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Offspring sex ratio studies of mammals: Does publication depend upon the quality of the research or the direction of the results?[1]

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Abstract: Alternative evolutionary hypotheses concerning a female's offspring sex ratio predict opposing deviations from unity. I suggest that researchers are more likely to attempt to publish sex ratio data when *post-hoc* analyses reveal significant deviations from unity, and that published studies reporting deviations from unity are more widely read than studies reporting no deviations. As a result, the scientific literature represents a biased sample of the occurrence of skewed offspring sex ratios in nature. The merits of sex ratio studies should be evaluated independently of the direction of the results or the presence of significant deviations from unity. Investigators must be encouraged to publish sex ratio data from long-term studies.
Keywords: sex ratio, publication bias, dominance.

Résumé: Des hypothèses alternatives donnent des prédictions opposées concernant l'écart à l'unité du rapport des sexes au sein de la progéniture d'une femelle. Nous formulons ici des propositions à l'effet que les chercheurs, à la suite d'analyses *post-hoc*, sont plus enclins à publier leurs données sur le rapport des sexes si celles-ci dévient significativement de l'unité et que, par ailleurs, les études rapportant des écarts significatifs par rapport à l'unité sont plus consultées que celles ne montrant aucune différence significative. Par conséquent, la littérature scientifique constitue un échantillon non-représentatif de l'occurrence des rapports de sexe biaisés en nature. On devrait évaluer le bien-fondé des études sur le rapport des sexes indépendamment des résultats ou de l'obtention d'écarts significatifs par rapport à l'unité. Les chercheurs devraient être encouragés à publier des données sur le rapport des sexes provenant d'études à long terme.
Mots-clés: rapport des sexes, biais de publication, dominance.

Introduction

Several evolutionary theories predict biases in offspring sex ratio, and many studies of mammals have reported that some females produce young with sex ratios different from unity. For example, when maternal care affects offspring fitness, mothers in good condition are predicted to produce more offspring of the sex requiring greater maternal care to achieve high fitness (Trivers & Willard, 1973), and some studies have supported this prediction (Gomendio *et al.*, 1990). However, few patterns of sex ratio bias appear to hold across species, even when ecological circumstances and putative selective pressures on sex ratio are similar (Clutton-Brock, 1991; Clutton-Brock & Iason, 1986). Some results from different studies of the same or similar species are at odds with each other. For example, dominant female red deer (*Cervus elaphus*), which are presumably in good body condition, produce significantly more sons than subordinate females (Clutton-Brock, Albon & Guinness, 1986), but well-nourished female white-tailed deer (*Odocoileus virginianus*) produce more daughters than females on a low nutritional plane (Verme, 1983; 1985). Dominant macaques have been reported to produce more sons or more daughters in different studies (Meikle, Tilford & Vessey, 1984; Silk, 1983; Silk *et al.*, 1981).

These opposite results provide support for alternative evolutionary hypotheses: one theory (Trivers & Willard, 1973) predicts that females in good condition will produce more sons, because they can give more care than females in poor condition. On the other hand, the Local Resource Competition theory (Silk, 1983) predicts that females in poor condition will produce more sons, because sons will emigrate and therefore are less likely than daughters to compete for resources in the mother's home range.

The goal of this comment is twofold. First, I suggest that because sex ratio data are easily analyzed *a posteriori*, the presence of significant deviations from unity may determine whether or not investigators attempt to publish these data, giving a false perception that sex ratios different from unity are widespread. Secondly, I argue that the visibility of the data (the reputation of the journal where they are published, how often they are cited or republished), and the prominence they are given in the article (for example, whether the title mentions sex ratio), are also dependent upon the direction of the results. Consequently, the amount of attention received by sex ratio studies may depend more upon the direction of their results than upon the quality of the study; by quality I mean sample size, completeness and accuracy of observations, duration of the study and ability to control for correlated variables. My aim is not to criticize any study or theory, but rather to encourage the publication of sex ratio data that show no difference from unity in circumstances where evolutionary theories would predict such deviations.

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Discussion

Before initiating a research program one should construct a falsifiable hypothesis, then test it. Testing sex ratio theories is likely the original goal of experimental studies, that manipulate the social environment or nutrition of individuals (Labov *et al*., 1986; Meikle *et al*., 1993; Verme & Ozoga, 1981). I suggest, however, that many non-manipulative research programs are not constructed to study variation in sex ratio, but collect information on sex ratio while researching other topics. Because sex ratio data are easily analyzed and because several theories predict deviations from unity, long-term data sets offer an easy opportunity to test these theories. Therefore, scientists who have collected these data sets may search for deviations from unity in sex ratios. I suggest that significant deviations from 1:1 are more likely to result in publication than non-significant deviations. If my suggestion is correct, published information is not a random sample of sex ratio data. Gurevitch *et al*. (1992) argued that meta-analysis could be an unbiased technique to evaluate scientific evidence gathered from literature reviews. Meta-analysis involves examining the results of different studies to assess whether they are consistent with each other and demonstrate a significant effect. This technique is likely a better alternative to "vote-count" literature reviews, but obviously only published results are available for analysis. If one type of result is more likely to be published, reviews will be unreliable (VanderWerf, 1992).

A similar argument could be put forth for almost any other subject in ecology: significant results are generally easier to publish. Editors must choose between manuscripts competing for limited journal space, and with non-significant results one can always suspect that inadequate sample sizes may be to blame. A bias towards publishing results only if they include statistically significant differences, however, is a particularly grave problem for observational sex-ratio studies, because the mechanisms for adaptive biases in sex ratio are not known and especially because deviations from unity in either direction could support plausible but competing evolutionary theories. Given a large number of observational studies that collect data on sex ratios, if the analyses are done *a posteriori*, about one in 10 should find significant (one-tailed) deviations from unity just by chance. One could then choose which theory predicts the results already obtained.

Studies reporting deviations in the direction predicted by evolutionary theories appear more likely to be brought to the attention of other scientists than studies that have found no differences, assuming that results of the latter kind are published. I will mention two examples, both on ungulates. Clutton-Brock and co-workers obtained data on the relationship between sex ratio and maternal dominance in red deer that fit the Trivers-Willard model. Those data have been widely published (Clutton-Brock, 1991; Clutton-Brock, Albon & Guinness, 1984; 1986; Clutton-Brock & Godfray, 1991; Clutton-Brock & Iason, 1986; Gomendio *et al*., 1990), yet their external validity is unknown because they are unreplicated in other populations of red deer. Recently, a study of pigs, set up specifically to experimentally test sex-ratio theories, reported similar results to those obtained for red deer (Meikle *et al.,* 1993). On the other hand, a data set for bighorn sheep (*Ovis canadensis*), from another long-term study (Festa-Bianchet, 1991), revealed a negative correlation between female dominance and sex ratio: whereas dominant hinds produce more sons, dominant ewes produce more daughters. Although I analyzed these data to test the Trivers and Willard model, I did not have that test as one of my goals when I began the study 10 years earlier. It is not unreasonable to suggest that fewer people noticed the bighorn data than saw the red deer data, even though both were the result of long-term studies of sexually dimorphic ungulates, were based upon similar sample sizes and had similar correlation coefficients (+0.44 and -0.42). My data were published in a paper that did not mention sex ratio in its title. Had I found a positive correlation, I wonder whether I would have tried to make those data into a paper of their own.

One important difference between the two studies is that dominance status is correlated with the reproductive success of red deer hinds but has no effect upon reproduction of bighorn ewes, so it is reasonable to expect a bias in offspring sex ratio in red deer and not in bighorn sheep. In another paper (Festa-Bianchet, 1989), I reported that ewes that produced a son one year were likely to produce a daughter the following year. I doubt that I would have reported the data if my analysis had revealed no effects, although I am encouraged because those results were duplicated in another sheep population (Bérubé, 1993).

A second example comes from studies of offspring sex ratio of bison (*Bison bison*) females in relation to reproductive status. Rutberg (1986) found that, as predicted by the Trivers-Willard model, cows that had not produced a calf the previous year were more likely to produce sons than cows that had a calf the previous year. This significant sex ratio bias was reported as support for the Trivers-Willard hypothesis, even though the same data set revealed that primiparous cows (mostly young and therefore small and subordinate) also produced an excess of males, a result contrary to the hypothesis. Another study (Green & Rothstein, 1991) of the same species found the opposite trend: cows produced more daughters after yield years than after parturient years, but the difference in sex ratio was not significant. That study also reported that sons of young cows were smaller than the sons of mature cows, suggesting that if primiparous cows controlled offspring sex they should produce more daughters, not sons as reported by Rutberg (1986). The Green & Rothstein paper did mention "sex" in its title, but was mostly about maternal investment. A similar data set showing no difference in sex ratio according to previous year's reproduction in bison was in a paper by Shaw & Carter (1989) about a different topic: sex ratio was not in the title. Again, it is likely that more researchers interested in sex ratio manipulation noticed the Rutberg data rather than the Green and Rothstein or the Shaw and Carter data. Another paper (Wolff, 1988) appeared to add support to the Trivers-Willard model but a rebuttal (Green & Berger, 1990) pointed out flaws in its methodology and presented data that showed no departure from unity in the sex ratio of offspring of bison cows.

Conclusion

In conclusion, I suggest that before we accept that adaptive variations in sex ratios are widespread as a result of natural selection we need more experimental studies that test specific predictions and results from replicated observational studies that actually agree with each other and with evolutionary theories on sex ratio manipulations. To achieve that goal, researchers and journal editors should be encouraged to publish sex ratio data from extensive and reliable studies, regardless of whether or not the data show significant deviations from unity. Large sample size and reliability of the data should be more important than presence or absence of statistical significance.

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Literature cited

Bérubé, C., 1993. L'investissement maternel différentiel en fonction du sexe du jeune chez le mouflon des Rocheuses (*Ovis canadensis*). M. Sc. Thesis, Département de biologie, Université de Sherbrooke, Sherbrooke, Québec.

Clutton-Brock, T. H., 1991. The Evolution of Parental Care. Princeton University Press, Princeton, New Jersey.

Clutton-Brock, T. H. & C. Godfray, 1991. Parental investment. Pages 234-262 *in* J. R. Krebs & N. B. Davies (ed.), Behavioural Ecology. Blackwell Scientific Publications, Oxford.

Clutton-Brock, T. H. & G. R. Iason, 1986. Sex ratio variation in mammals. Quarterly Review of Biology, 61: 339-374.

Clutton-Brock, T. H., S. D. Albon & F. E. Guinness, 1984. Maternal dominance, breeding success and birth sex ratios in red deer. Nature, 308: 358-360.

Clutton-Brock, T. H., S. D. Albon & F. E. Guinness, 1986. Great expectations: Dominance, breeding success and offspring sex ratio in red deer. Animal Behaviour, 34: 460-471.

Festa-Bianchet, M., 1989. Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). Journal of Animal Ecology, 58: 785-795.

Festa-Bianchet, M., 1991. The social system of bighorn sheep: Grouping patterns, kinship and female dominance rank. Animal Behaviour, 42: 71-82.

Gomendio, M., T. H. Clutton-Brock, S. D. Albon, F. E. Guinness & M. J. Simpson, 1990. Mammalian sex ratios and variation in costs of rearing sons and daughters. Nature, 343: 261-263.

Green, W. C. H. & J. Berger, 1990. Maternal investment in sons and daughters: Problems of methodology. Behavioral Ecology and Sociobiology, 27: 99-102.

Green, W. C. H. & A. Rothstein, 1991. Sex bias or equal opportunity? Patterns of maternal investment in bison. Behavioral Ecology and Sociobiology, 29: 373-384.

Gurevitch, J., L. L. Morrow, A. Wallace & J. S. Walsh, 1992. A meta-analysis of competition in field experiments. American Naturalist, 140: 539-572.

Labov, J. B., U. W. Huck, P. Vaswani & R. D. Lisk, 1986. Sex ratio manipulation and decreased growth of male offspring of undernourished golden hamsters (*Mesocricetus auratus*). Behavioral Ecology and Sociobiology, 18: 241-249.

Meikle, D. B., L. C. Drickamer, S. H. Vessey, T. L. Rosenthal & K. S. Fitzgerald, 1993. Maternal dominance and secondary sex ratio in domestic swine. Animal Behaviour, 46: 79-85.

Meikle, D. B., B. L. Tilford & S. H. Vessey, 1984. Dominance rank, secondary sex ratio, and reproduction of offspring in polygynous primates. American Naturalist, 124: 173-188.

Rutberg, A. T., 1986. Lactation and fetal sex ratios in American bison. American Naturalist, 127: 89-94.

Shaw, J. H. & T. S. Carter, 1989. Calving patterns among American Bison. Journal of Wildlife Management, 53: 896-898.

Silk, J. B., 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive activities. American Naturalist, 130: 56-66.

Silk, J. B., C. B. Clark-Weatley, P. S. Rodman & A. Samuels, 1981. Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques (*Macaca radiata*). Animal Behaviour, 29: 1106-1120.

Trivers, R. L. & D. E. Willard, 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science, 179: 90-92.

VanderWerf, E., 1992. Lack's clutch size hypothesis: An examination of the evidence using meta-analysis. Ecology, 73: 1699-1705.

Verme, L. J., 1983. Sex ratio variation in *Odocoileus*: A critical review. Journal of Wildlife Management, 47: 573-582.

Verme, L. J., 1985. Progeny sex ratio relationships in deer: Theoretical *vs*. observed. Journal of Wildlife Management, 49: 134-136.

Verme, L. J. & J. J. Ozoga, 1981. Sex ratio of white-tailed deer and the estrus cycle. Journal of Wildlife Management, 45: 710-715.

Wolff, J. O., 1988. Maternal investment and sex ratio adjustment in American bison calves. Behavioral Ecology and Sociobiology, 23: 127-133.