Applied Animal Behaviour Science xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

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

The Wood-Gush legacy: A sociobiology perspective to fertility and welfare in chickens

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ARTICLE INFO

Article history:
Received 19 August 2015
Received in revised form
14 December 2015
Accepted 6 January 2016
Available online xxx

Keywords:
Sexual selection
Sexual conflict
Inclusive fitness
Animal welfare
Fertility
Gallus

ABSTRACT

Wood-Gush's seminal work on the social behaviour and welfare of fowl populations laid the foundations of a sociobiology approach to understand the evolutionary nature of social interactions and their applied significance for domestic animals. Within this context, maintaining high fertility and welfare standards pose key challenges. Reviewing recent advances in the study of sexual behaviour in the fowl, I discuss how the fertility and welfare of domestic populations are inter-related and how both can be improved by resolving the forces that drove the evolution of complex sexual behaviour before domestication. I argue that this resolution hinges on three fundamental tools of sociobiology: sexual selection, sexual conflict and inclusive fitness.

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> *"As an agricultural animal the domestic fowl is of increasing economic importance in the highly-developed countries, and many of its husbandry problems concern its behaviour."*
>
> Wood-Gush (1971). *The Behaviour of the Domestic Fowl*. Heinemann Educational Books Ltd., London, p. 1.

1. Introduction

Wood-Gush's words more than 40 years ago were remarkably prescient. Over the last decades poultry production has increased exponentially as poultry consumption has taken over consumption of other meat types in several industrialised countries, and intensive poultry production is expanding rapidly world-wide (e.g. Laughlin, 2009). Currently, more than 50 billion birds are estimated to be produced annually around the world with increasingly efficient production and artificial selection regimes. Over the same period of time however, two factors have emerged as formidable constraints to this development: the maintenance of high fertility, both at the level of the population and at the level of individual sires within populations, and the welfare of the animal produced (Ellen et al., 2014). Through his pioneering studies of fowl populations, Wood-Gush was one of the first biologists to identify the importance of these issues and to recognize the pivotal role of social behaviour. The overarching goal of this review is to build on Wood-Gush's legacy to argue, in light of recent empirical work in fowl populations, that social behaviour relates fertility with welfare, and that maintaining high standards in both hinges on an evolutionary understanding of the social behaviour of domestic animals.

In this review, I use the term fertility as a measure of reproductive fitness.

From the perspective of individual females, fertility corresponds to the proportion of ova produced that is converted into zygotes through successful mating. Standardized variance in female fertility therefore generates an opportunity for selection on females over securing sufficient sperm supplies and their efficient storage, which may or may not involve an element of intra-sexual competition. From the perspective of individual males, fertility corresponds to the overall number of zygotes sired, and standardized variance reflects largely an opportunity for sexual selection on male ability to outcompete each other over reproductive opportunities. This distinction is helpful in that it immediately follows that, while maximizing the fertility of the population as a whole requires maximizing the fertility of individual females, the fitness interests of individual males are not necessarily aligned with those of individual females and of the population as a whole. Below, I discuss scenarios in which male and female interests are in conflict (sexual conflict, see below) and their implications for fertility and welfare in animal production. Similarly, I use a functional definition of animal welfare based on the needs of an animal to display behaviours,

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http://dx.doi.org/10.1016/j.applanim.2016.01.025
0168-1591/© 2016 Published by Elsevier B.V.

Please cite this article in press as: Pizzari, T., The Wood-Gush legacy: A sociobiology perspective to fertility and welfare in chickens. Appl. Anim. Behav. Sci. (2016), http://dx.doi.org/10.1016/j.applanim.2016.01.025

originally evolved within a context in which individuals operate as agents of inclusive fitness maximization. The purpose of this is to review the range of natural social behaviours expressed by an animal with an understanding of their evolutionary significance. In particular, this definition enables us to recognize that the repertoire of social behaviours may include inclusive fitness strategies that benefit a focal individual indirectly by favouring relatives (see below).

Traditionally, livestock fertility and welfare have been treated as factors largely determined by the genotype of an individual. Consequently, artificial selection acting on additive variance underlying these traits have been the main tool to improve fertility and welfare of domestic animal populations. However, as Wood-Gush had intuited, the fertility and welfare of an individual are in fact social traits, largely influenced by its interactions with other members of the population. The social nature of these traits explains why, while artificial selection has achieved tremendous results in traits that are less influenced by social interactions such as body size, growth rate, feed conversion, and fecundity (e.g. Etches, 1996), the evolutionary response of fertility (Laughlin, 2009) and welfare (see review in Muir and Craig, 1998) has been less consistent.

The reason for this discrepancy is that such interactions are often complex – i.e. the fitness of an individual is influenced by the outcome of interactions amongst multiple individuals and the identity of these individuals- and plastic – i.e. the behaviour of an individual changes in response to the social context and the identity of its interactants. While new quantitative genetic approaches are being developed which take into explicit consideration indirect genetic effects arising from social interactions (e.g. Wade et al., 2010; Ellen et al., 2014), the relative role of the social environment in fertility and welfare remains little understood. This gap is significant given that calls to determine the relative roles of genes and environment in animal welfare date back more than 10 years ago (e.g. Moberg and Mench, 1993).

Their close link with fitness indicates that traits associated with fertility and welfare have been moulded by Darwinian natural selection long before the relatively recent intervention of domestication and artificial selection. Wood-Gush was one of the first to appreciate that in order to understand social behaviour in domestic animals it is critical to first establish how such behaviour has evolved under natural selection before domestication. Only after the functional significance of behaviour is elucidated under natural conditions, can we begin to study how domestication and artificial selection operate on the naturally-selected substrate to drive change. The fowl represents a particularly poignant case in point.

1.1. The fowl study system

The genus *Gallus* comprises of four species widely distributed in South-East Asia, the red junglefowl, *Gallus gallus*, the gray junglefowl *Gallus sonneratii*, the Sri Lankan junglefowl, *Gallus lafayettii*, and the green junglefowl, *Gallus varius*. Early molecular work indicated that the domestic fowl, *Gallus domesticus*, has a monophyletic origin, arising from a single subspecies of the red junglefowl (Fumihito et al., 1994, 1996). More recent work however, has shown evidence that some introgression with at least the gray junglefowl may have occurred in the early stages of domestication (Eriksson et al., 2008).

Domestication started around 9000 years ago in India and China (Wood-Gush, 1959), and a range of different breeds were well known from the classic period, indicating consistent programmes of artificial selection. The industrial revolution catalyzed the advent of intensive farming and intense selection for production traits (Wood-Gush, 1959; Etches, 1996). The study of the behaviour of red junglefowl, and domestic fowl, *G. domesticus*, begun in the 40s and 50s with pioneers such as Allee, Collias and Collias, and Guhl, and was catalyzed in the 60s and 70s by the work of Wood-Gush, Kruijt, McBride, and several others. More recently, this approach has served as a platform for systematic comparisons between ancestral and derived populations with a range of inter-related foci, including domestication and its genetic architecture (e.g. Jensen, 2014), and mate choice and reproductive behaviour (e.g. Zuk et al., 1990; Pizzari et al., 2002). This body of work indicates that domestic fowl have retained behavioural patterns that are broadly speaking qualitatively (but not necessarily quantitatively) similar to those observed in red junglefowl. Under natural conditions, populations of red junglefowl and feral populations of domestic fowl, display a social structure in which interactions within social groups are governed by a tight sex-specific dominance hierarchy. Social status plays a consequently important role in competition over resources including reproductive opportunities. Studies of red junglefowl in the wild describe social units in which a dominant male defends a harem of females from multiple satellite, subordinate males (Collias et al., 1964; Collias and Collias, 1967; see also McBride et al., 1969; Collias and Collias, 1996; Sullivan, 1991 for description of similar structures in captive red junglefowl populations and feral populations of domestic fowl). Social groups are therefore typically characterized by a polygynandrous mating system, in which despite the monopoly of multiple females exercised by dominant males (harem polygyny), females can mate with more than one male and will typically do so (polyandry). In the following sections, I aim to review recent work relevant to fertility and animal welfare within the context of three inter-related theoretical sociobiology frameworks, namely: (i) sexual selection, (ii) sexual conflict, and (iii) inclusive fitness.

2. Sexual selection

Darwin (1871) famously defined sexual selection as a selective process acting on individual variation in reproductive success due to competition over mating and fertilization among members of the same sex and species. The evolution of anisogamy has naturally predisposed the male sex to relatively high variation in reproductive success and thus relatively high opportunity for sexual selection (Bateman, 1948; Trivers, 1972; Andersson, 1994; Kokko et al., 2006; Parker and Pizzari, 2015). The total reproductive success of males (T) can be decomposed into three multiplicative constituents as follows:

$$T = (M \times N \times P) + \varepsilon$$

where M represents the number of mating partners (i.e. females), N, their average fecundity (i.e. clutch size), P, the proportion of the ova produced by his mating partners that a male fertilizes and ε is an error with 0 mean (Parker and Pizzari, 2015). Competition over access to females and particularly over more fecund females (i.e. M and N) generates opportunity for premating (or precopulatory) sexual selection. In internally-fertilising species on the other hand, competition to fertilise the ova of a female (P) occurs after mating when females mate with multiple partners (i.e. females are polyandrous) and the sperm of different males have the opportunity to fertilise the same ova, generating potential for postmating (or postcopulatory) sexual selection. Variance in male reproductive success therefore has a complex architecture determined by variance in pre- and postmating sources and their respective covariances (Collet et al., 2012). Sexual selection can then be measured on individual traits to the extent to which they covary with these reproductive components.

A significant portion of variation in male reproductive success in fowl populations is explained by male social status with dominant males siring more offspring than their subordinates (Guhl et al., 1945; Guhl and Warren, 1946; Jones and Mench, 1991; Collet et al.,

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