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Distinguishing cooperation from cohabitation: the feral horse case study

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The possibility that unrelated polygynous males cooperate to breed intrigues behavioural ecologists (e.g. baboons, *Papio anubus*: Packer 1977; Noë 1992; lions, *Panthera leo*: Bygott et al. 1979; Packer et al. 1988; Grinnell et al. 1995; oribi, *Ourebia ourebia*: Arcese 1999; horses, *Equus caballus*: Feh 1999). Unfortunately, showing that males that cohabit also cooperate is difficult (Jamieson & Craig 1987; Dugatkin et al. 1992; Heinsohn & Legge 1999). Cooperation is defined as an outcome that, despite individual costs, is advantageous for the members of a group of two or more individuals and the achievement of which requires some type of collective action (Dugatkin et al. 1992). Therefore, to demonstrate cooperation, researchers must measure more than just the behaviours that might occur just because males live together (e.g. intermale aggression and affiliation, female defence and mating by all males), and a positive relationship between cohabitation and reproductive success. They must also provide evidence for the behavioural mechanism by which reproductive success, and eventually inclusive fitness, is improved. That is, both proximate (behavioural and/or physiological) and ultimate (evolutionary) mechanisms must be shown to exist and function together. Furthermore, when making comparisons of the behaviour and reproductive success of so-called cooperators and noncooperators in a population, researchers must ensure they are comparing groups of individuals that are equivalent in every other way, or that they control for any other associated and confounding differences. Moreover, cooperators and noncooperators, and their behaviour, should not be defined a posteriori according to the presence or absence of a cohabitant male, but rather by operational definitions of behaviours

determined a priori and subsequently measured for evidence of cooperation.

While it is difficult to prove cooperation between animals, it is much simpler to disprove it. Indeed, non-cooperation should be the null model (Harvey et al. 1983; Conner & Simberloff 1986) in tests of cooperation hypotheses. We suggest that in the search for male cooperation, authors seldom test this null model, have been too quick to conclude that cooperation between cohabitating males occurs, and that much of the behavioural evidence used may also support other hypotheses for cohabitation besides cooperation. We use the literature that compares single and multistallion breeding groups in feral horses as a case study to illustrate how enthusiasm for the concept of cooperation between unrelated polygynous males can lead to premature support for it.

Stallion Cooperation

Feral horse breeding structure throughout the world is typical of female defence polygyny. The breeding group, called a band, includes from 1 to 26 mares, their pre-dispersal offspring, and usually one, but up to five, stallions who defend the mares from other stallions all year round. Stallions that are not members of bands are called bachelors, and live alone and in ephemeral all-male groups. Multistallion bands are ubiquitous in feral populations irrespective of the population's habitat and density as long as the adult sex ratio is not extremely female biased because of stallion removals (Linklater, 2000). The stallions in multistallion bands are not necessarily related and have a strongly hierarchical relationship. The subordinate stallion contributes disproportionately to mare group defence but copulates less often with mares in the band, thereby obtaining some paternity but less than the dominant stallion (Feh 1999). Both single and multistallion breeding groups occupy

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nonexclusive home ranges and are therefore sympatric. Thus, feral horse populations offer the opportunity to test cooperation hypotheses.

In the absence of kin-selected benefits, by-product mutualism and reciprocal altruism hypotheses have been proposed to explain the presence of multistallion bands. For example, it has been suggested that subordinate stallions increase the stability of mare groups and band size. Where band dominance varies positively with band size, the larger, more stable, multistallion bands were thought to gain better access to limited resources, thereby enhancing the lifetime reproductive success of the band's stallions (Miller 1979, 1981; Franke Stevens 1990). Subordinate stallions were also thought to benefit from improved grazing and experience, greater paternity and an increased chance of inheriting a band compared with bachelors (Rubenstein 1982; Franke Stevens 1990; Feh 1999). Furthermore, it has been suggested that the dominant stallion may benefit from the subordinate's help in mare defence thus ensuring his hegemony with a mare group, allowing him more time for grazing and reduced effort in mare defence (Rubenstein 1982; Feh 1999). Where these factors contribute to net benefits for all stallions in a band then the mechanism for the origin and maintenance of their relationship is called by-product mutualism (Dugatkin 1997).

However, Berger (1986) argued that stallions in multistallion bands 'did not confer greater reproductive advantage per male' and Feh (1999) confirmed this by showing that individual stallions in multistallion bands obtain less paternity than stallions in sympatric single-stallion bands. Berger (1986) described an age differential between stallions in multistallion bands and called their relationship a defensive alliance. Unfortunately, Berger (1986) was unable to determine whether resident dominant males tolerated the proximity of another male because he cooperated (reciprocal altruism; Dugatkin 1997) or whether males that were too old to defend a mare group alone adopted the alternative subordinate stallion behaviour (mate parasitism or best-of-a-bad-job strategy; Dunbar 1982). Berger (1986) provided an interesting and valuable interpretation of multistallion band observations because he was explicit about the limitations of his data.

Feh (1999) also called the relationship between stallions in bands an alliance. She showed that the stallions that share mare groups obtain less paternity than stallions defending a mare group alone and that subordinate stallions obtain much less paternity than the dominant stallion; she also claimed to show that subordinate stallions obtain more paternity than comparable stallions who are bachelors. She concluded that the stallion relationship is based on mutualism with elements of reciprocity between inferior, lower-ranked, stallions. Feh (1999) was the first to present supporting measures of paternity and therefore provide the means to test for a functional relationship between the behaviour of stallions and their reproductive success. She used paternity data to suggest that lower-ranked stallions form an alliance with another stallion in a band, rather than remain a bachelor, to increase

their reproductive success and ultimately their inclusive fitness.

The Problem

The literature supporting cooperation between stallions in feral horses illustrates the typical shortcomings in the evidence for cooperation. Furthermore, we think Feh's (1999) experimental design and use of paternity data provides an example of analytical flaws that others making intraspecific comparisons to test cooperation hypotheses may find instructive.

Cooperation hypotheses require that there are selective benefits for stallions that participate in multistallion breeding groups. These benefits have been judged in the past by comparing the subordinate stallions in multistallion bands with stallions that are bachelors, and the stallions that are dominant in multistallion bands with those that defend a mare group alone (e.g. Feh 1999). In particular, the comparison between subordinate stallions and bachelors is crucial. It may provide the functional explanation for why a stallion would be part of a multistallion band as a subordinate, where he must contribute most to mare defence but obtain significantly less paternity than all other band stallions, rather than remain a bachelor who may obtain opportunistic paternity and later obtain a mare group of his own.

Prior to Feh (1999), none of the authors who proposed selective benefits to stallions that cohabit in multistallion bands (e.g. Miller 1979, 1981; Rubenstein 1982; Berger 1986; Franke Stevens 1990) quantified a causative relationship between apparent proximal benefits and a fitness parameter such as increased reproductive success. Indeed, even some of the proximal benefits were not measured but assumed (e.g. better access to limited resources, Miller 1979, 1981; inheritance of mares by the subordinate, Rubenstein 1982; Franke Stevens 1990; improved experience, occasional copulations and better grazing for the subordinate, Rubenstein 1982). Moreover, paternity and fecundity data in Bowling & Touchberry (1990), Eagle et al. (1993) and Linklater et al. (1999), and the experimental removal of subordinate stallions (Linklater 1998; Linklater et al. 1998), indicate that multistallion breeding groups may not provide greater reproductive advantages, and may actually constitute a reproductive cost for both dominant and subordinate stallions in multistallion bands, when compared with equivalent stallions that are not cooperating.

For example, a similar proportion of foals in single and multistallion bands were not sired by the resident stallion(s) (single stallion 24%, multistallion 22%). In 55% of single-stallion bands all the foals were sired by the resident stallion which compares favourably with the 52% of foals sired by the dominant stallion in multistallion bands. Moreover, in only 26% of multistallion bands was the paternity shared between the stallions, yet, on average, 33% of foals in all bands were sired by nonband, and therefore possibly bachelor, stallions (Bowling & Touchberry 1990). Furthermore, Eagle et al. (1993) showed that if the dominant stallions in multistallion bands were vasectomized, subsequent foaling

rates were reduced indicating that the dominant stallion was successful in limiting the paternity that subordinates obtained even though the mares they mated failed to conceive and therefore cycled repetitively until winter anoestrus. In addition, Linklater et al. (1999) showed that the fecundity of mares in multistallion bands was significantly poorer than for mares in single-stallion bands because of suppressed fertility and greater offspring mortality. They attributed the difference to elevated rates of harassment of mares by stallions that resulted from the competitive relationship between the stallions in multistallion bands. Where two or more stallions defended the same mare group the rates of stallion aggression towards mares, and subsequent rates of mare displacement, were seven and four times higher, respectively, than those measured in single-stallion bands. Linklater et al.'s (1999) conclusion is consistent with that of Berger (1983) and Kaseda et al. (1995) who attributed the poor reproductive success of mares to the harassment associated with their social dispersal. Lastly, an experiment in which subordinate stallions were removed temporarily from multistallion bands showed that the dominant stallion was capable of defending and maintaining the mare group without subordinate 'help'. Multistallion breeding groups from which subordinate stallions had been removed did not lose mares nor was the remaining stallion displaced, although high rates of interband interaction meant that there were numerous opportunities for these to occur (Linklater 1998).

These studies suggest the following.

(1) Multistallion breeding groups provide relatively fewer reproductive opportunities for resident stallions because they suppress mare fertility and have greater offspring death.

(2) Some subordinate stallions may actually be obtaining similar or less paternity than opportunistic bachelors of the same age who do not incur the costs and risks of mare defence in a band.

(3) Subordinate stallions do not reduce paternity loss by cuckoldry or mare out-breeding, or mare loss, from multistallion bands. Thus, their 'help' in mare defence appears to be ineffectual.

(4) Dominant stallions in multistallion bands obtain relatively less paternity than the stallions of single-stallion bands although they are also capable of defending their mare group alone.

Therefore, the selective benefits for cohabitation by cooperation between stallions appear to be, at best, weak. We conclude that the prerequisites for cooperation are probably absent. Researchers working with feral horses should be wary of presuming the functional significance of multistallion relationships and behaviours in breeding groups before they can show quantitatively that the prerequisites are present (i.e. proximal benefit causing greater paternity and leading to increased lifetime reproductive success).

Our conclusion here is very different to Feh's (1999), from her work with Camargue horses. Crucial to Feh's (1999) cooperative conclusion is that the subordinate stallions, which are presumed to be unable to defend a

mare group alone, do indeed gain reproductive advantages by forming an alliance with a dominant stallion that they would not otherwise obtain by remaining a bachelor. Feh (1999) showed that subordinate stallions in alliances had significantly greater paternity than bachelors *prima facie*. However, all of Feh's (1999) bachelor males were of prereproductive age (i.e. less than 4 years old) when they became bachelors after natal dispersal (\bar{X} =2.4 years old, range 1–3) and remained bachelors for an average of less than 2 years. Subordinate stallions in multistallion bands, on the other hand, were of reproductive age (\bar{X} =4 years, range 3–5) when they formed an 'alliance' and remained in the alliance until up to 9 years of age (Figure 1 in Feh 1999).

Although domestic stallions reach puberty before the end of their second year (Evans et al. 1990), they are not physically, physiologically and behaviourally mature until at least 4 years of age and often do not form stable breeding relationships with mares and thus form a band until their fifth or sixth year in feral populations (Hoffmann 1985; Berger 1986; Feh 1990, 1999). Consequently, the difference in the reproductive success of bachelors and subordinate stallions in the Camargue population, as presented by Feh (1999), may be better understood by the relative age and maturity of the two groups. To show that the subordinate stallion in a multistallion band is adopting cooperative behaviour to increase his reproductive success, a comparison between bachelors and subordinates of the same reproductive maturity, or at least age, would be necessary. Such a comparison was not made. For intraspecific comparisons between individuals in different reproductive contexts, the individuals must be legitimately comparable or age and maturity must be controlled for.

Consequently, we have reservations about the use of cooperative hypotheses to account for multistallion bands in feral horses. Our critique suggests that the paternity data, as presented by Feh (1999), cannot be used to support the use of the terms alliance, mutualism or reciprocal altruism to describe the relationship between stallions. This is not to say that Camargue stallions do not cooperate. Indeed, Feh (1999) showed that where two Camargue stallions live with the same mare group they have an associative and affiliative relationship. Such a relationship is different from the agonistic and extreme social and spatial hierarchy between stallions in multistallion bands in other populations (e.g. Miller 1981; Berger 1986; Franke Stevens 1990; Linklater, 2000) and warrants further investigation. However, Feh (1999) did not provide evidence that stallions that cohabit in breeding groups are indeed cooperating, or that cooperation is the basis for the formation and maintenance of multistallion bands in feral horse populations. At best the problem requires paternity data to be applied more judiciously by controlling for stallion age to test the hypothesis that multistallion relationships are reproductively beneficial for the subordinate stallions.

A Solution?

First, we suggest that the problem with Feh's (1999) analysis might have been avoided if stallion behaviour

had been defined independently of its context or the characteristics of the participants by using operational rather than conceptual definitions (Hailman 1982; e.g. Mitchell 1990). Second, premature conclusions of cooperation between stallions might have been avoided if Feh (1999) had explicitly tested the null hypothesis that stallions are not cooperating. Third, premature conclusions of cooperation might have been avoided if the question 'How do stallion relationships and multistallion bands form and function?' was answered first and only then was the question 'What is the selective advantage of the relationship between stallions?' considered, if it still proved to be an appropriate question.

The strength of this approach is three-fold. First, the operational definition of behaviour allows males to be classified according to their behaviour rather than into otherwise arbitrary behavioural and reproductive categories (e.g. bachelor, sneak, follower, subordinate, satellite and dominant, Wirtz 1982; Dunbar 1984; Feh 1999). For example, Feh (1999) categorized stallions into bachelor, subordinate or dominant in a multistallion band, and single-stallion behavioural classes based on their social context rather than defining them quantitatively from their behaviour. Consequently, stallions that did not differ in their behavioural repertoire and who used all behaviours and reproductive strategies with time, maturity and experience (Figure 1 in Feh 1999) were placed into separate reproductive categories. The classification into discrete reproductive classes of males whose behaviour varies continuously because of their maturity and experience is not confined to studies of horses but has been a common feature in studies of mammalian mating systems (e.g. Wirtz 1982; Dunbar 1984; Rubenstein 1986; Hogg & Forbes 1997; Arcese 1999). Second, the operational definition of behaviour avoids tautological explanations where the definition of the behaviour presupposes its cause (see Tinbergen 1963 on 'neutral terminology'). For example, aggressive behaviour between stallions from different bands has been called 'helping' when one of them is a subordinate stallion in a multistallion band (Berger 1986; Feh 1999). However, the 'helper' may behave no differently from a stallion defending a mare group alone or a mature bachelor opportunistically defending a mare separated from her band. Third, this approach does not make the assumption that current utility implies adaptive value or betrays the phenotype's ultimate causation. Such an assumption is not always justified (Hailman 1982; Byers & Bekoff 1990; Byers 1997).

Nevertheless, this approach requires a more thorough understanding of the ontogeny of social behaviour and breeding groups and it is a field that is poorly developed in sociobiology (Lott 1984, 1991; but see Moore et al. 1998; Veissier et al. 1998). Although sociobiologists accept that intraspecific differences in social and breeding group structure may be better explained by differences during behavioural or group development, the role of behavioural and breeding group ontogeny is rarely considered (but see Jamieson & Craig 1987; Jamieson 1989). Indeed, some have cautioned that by viewing different

social systems as mixed traits we ignore behavioural ontogeny, learning processes and the developmental aspects of social and breeding structure (Hailman 1982; Lott 1984) which may also contribute to variation in mating systems.

We suggest that stallion behavioural and breeding group ontogeny may explain variation in the numbers of stallions in bands better than cooperation hypotheses. After natal dispersal, individual stallions pass through a sequence of breeding contexts that include bachelor groups, multistallion and single-stallion bands as they mature and gain experience. The most mature and experienced stallions are more likely to have mare groups to themselves while juvenile stallions are more likely to be bachelors in all-male groups. Therefore, there is a continuum of social contexts for stallions that appear to correlate with their age and perhaps experience that includes multistallion bands (for example, see Figure 1 in Feh 1999). Therefore, multistallion bands may be a product of stallion behavioural ontogeny and band ontogeny rather than selection for cooperative behaviour. Therefore, in studies of sympatric single and multimale breeding systems we recommend that researchers focus on describing how single and multimale breeding groups and male relationships form and function. In this regard, it would be useful for observers to describe the sequence of events and behaviours that result in the formation of multimale compared with single-male breeding groups. Lastly, we suggest that more male removal experiments (e.g. Linklater 1998; Linklater et al. 1998) would be useful to determine the form and dependence of the relationships between males, and males and females, in multimale bands and enable a more direct test of cooperation hypotheses. Our purpose is not to decry studies that have suggested that feral stallions may cooperate or suggest that their conclusion is necessarily incorrect. Rather, we aim to demonstrate the problems with many analyses of cooperation that may be avoided if a different approach is used and that other explanations for male cohabitation, aside from cooperation, are equally possible and testable, but are considered less.

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References

- Arcese, P. 1999. Effect of auxiliary males on territory ownership in the oribi and the attributes of multimale groups. *Animal Behaviour*, **57**, 61–71.
- Berger, J. 1983. Induced abortion and social factors in wild horses. *Nature*, **303**, 59–61.
- Berger, J. 1986. *Wild Horses of the Great Basin*. Chicago: University of Chicago Press.

- Bowling, A. T. & Touchberry, R. W.** 1990. Parentage of Great Basin feral horses. *Journal of Wildlife Management*, **54**, 424–429.
- Byers, J. A.** 1997. *American Pronghorn: Social Adaptations and Ghosts of Predators Past*. Chicago: University of Chicago Press.
- Byers, J. A. & Bekoff, M.** 1990. Inference in social evolution theory: a case study. In: *Interpretation and Explanation in Evolution and Adaptation. Vol. II: Explanation, Evolution and Adaptation* (Ed. by M. Bekoff & D. Jamieson), pp. 84–97. Boulder, Colorado: Westview Press.
- Bygott, J. D., Bertram, B. C. R. & Hanby, J. P.** 1979. Male lions in large coalitions gain reproductive advantages. *Nature*, **282**, 839–841.
- Conner, E. F. & Simberloff, D.** 1986. Competition, scientific method, and null models in ecology. *American Scientist*, **74**, 155–162.
- Dugatkin, L. A.** 1997. The evolution of co-operation, four paths to the evolution and maintenance of cooperative behaviour. *Bioscience*, **47**, 355–362.
- Dugatkin, L. A., Mesterton-Gibbons, M. & Houston, A. I.** 1992. Beyond the prisoner's dilemma, toward models to discriminate among mechanisms of cooperation in nature. *Trends in Ecology and Evolution*, **7**, 202–205.
- Dunbar, R. I. M.** 1982. Intra-specific variations in mating strategy. In: *Perspectives in Ethology. Vol. 5* (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 385–431. New York: Plenum.
- Dunbar, R. I. M.** 1984. *Reproductive Decisions: an Economic Analysis of Gelada Baboon Social Strategies*. Princeton, New Jersey: Princeton University Press.
- Eagle, T. C., Asa, C. S., Garrott, R. A., Plotka, E. D., Siniff, D. B. & Tester, J. R.** 1993. Efficacy of dominant male sterilisation to reduce reproduction in feral horses. *Wildlife Society Bulletin*, **21**, 116–121.
- Evans, J. W., Barton, A., Hintz, H. F. & Van Vleck, L. D.** 1990. *The Horse*. New York: W. H. Freeman.
- Feh, C.** 1990. Long term paternity data in relation to different rank-aspects for Camargue stallions. *Animal Behaviour*, **40**, 995–996.
- Feh, C.** 1999. Alliances and reproductive success in Camargue stallions, *Equus caballus*. *Animal Behaviour*, **57**, 705–713.
- Franke Stevens, E.** 1990. Instability of harems of feral horses in relation to season and presence of subordinate stallions. *Behaviour*, **112**, 149–161.
- Grinnell, J., Packer, C. & Pusey, A. E.** 1995. Cooperation in male lions, kinship, reciprocity or mutualism? *Animal Behaviour*, **49**, 95–105.
- Hailman, J. P.** 1982. Ontogeny: toward a general theoretical framework for ethology. In: *Perspectives in Ethology. Vol. 5* (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 133–189. New York: Plenum.
- Harvey, P. H., Colwell, R. K., Silvertown, J. W. & May, R. M.** 1983. Null models in ecology. *Annual Review of Ecology and Systematics*, **14**, 189–211.
- Heinsohn, R. & Legge, S.** 1999. The cost of helping. *Trends in Ecology and Evolution*, **14**, 53–57.
- Hoffmann, R.** 1985. On the development of social behavior in immature males of a feral horse population (*Equus przewalskii f. caballus*). *Zeitschrift für Säugetierkunde*, **50**, 302–314.
- Hogg, J. T. & Forbes, S. H.** 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk 'unconventional' tactic. *Behavioral Ecology and Sociobiology*, **41**, 33–48.
- Jamieson, I. G.** 1989. Behavioral heterochrony and evolution of birds: helping at the nest an unselected consequence of communal breeding? *American Naturalist*, **133**, 394–406.
- Jamieson, I. G. & Craig, J. L.** 1987. Critique of helping behaviour in birds: a departure from functional explanations. In: *Perspectives in Ethology. Vol. 7* (Ed. by P. Bateson & P. Klopfer), pp. 79–98. New York: Plenum.
- Kaseda, Y., Khalil, A. M. & Ogawa, H.** 1995. Harem stability and reproductive success of Misaki feral mares. *Equine Veterinary Journal*, **27**, 368–372.
- Linklater, W. L.** 1998. The social and spatial organisation of horses. Ph.D. thesis, Massey University, Palmerston North, New Zealand.
- Linklater, W. L.** 2000. Adaptive explanations in socio-ecology: lessons from the Equidae. *Biological Reviews*, **75**, 1–20.
- Linklater, W. L., Cameron, E. Z., Stafford, K. J. & Austin, T.** 1998. Chemical immobilisation and temporary confinement of two Kaimanawa feral stallions. *New Zealand Veterinary Journal*, **46**, 117–118.
- Linklater, W. L., Cameron, E. Z., Minot, E. O. & Stafford, K. J.** 1999. Stallion harassment and the mating system of horses. *Animal Behaviour*, **58**, 295–306.
- Lott, D. F.** 1984. Intra-specific variation in the social systems of wild vertebrates. *Behaviour*, **88**, 266–325.
- Lott, D. F.** 1991. *Intra-specific Variation in the Social Systems of Wild Vertebrates*. Cambridge: Cambridge University Press.
- Miller, R.** 1979. Band organisation and stability in Red Desert feral horses. In: *Symposium on the Ecology and Behavior of Wild and Feral Equids* (Ed. by R. H. Denniston), pp. 113–128. Laramie: University of Wyoming.
- Miller, R.** 1981. Male aggression, dominance and breeding behavior in Red Desert feral horses. *Zeitschrift für Tierpsychologie*, **57**, 340–351.
- Mitchell, S. D.** 1990. The units of behavior in evolutionary explanations. In: *Interpretation and Explanation in the Study of Animal Behavior. Vol. II: Explanation, Evolution and Adaptation* (Ed. by M. Bekoff & D. Jamieson), pp. 63–83. Boulder, Colorado: Westview Press.
- Moore, M. C., Hews, D. K. & Knapp, R.** 1998. Hormonal control and evolution of alternative male phenotypes: generalizations of models for sexual differentiation. *American Zoologist*, **38**, 133–151.
- Noë, R.** 1992. Alliance formation among male baboons: shopping for profitable partners. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 285–321. Oxford: Oxford University Press.
- Packer, C.** 1977. Reciprocal altruism in *Papio anubus*. *Nature*, **265**, 441–443.
- Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, S. J. & Borgerhoff-Mulder, M.** 1988. Reproductive success of lions. In: *Reproductive Success* (Ed. by T. H. Clutton-Brock), pp. 363–383. Chicago: University of Chicago Press.
- Rubenstein, D. I.** 1982. Reproductive value and behavioural strategies, coming of age in monkeys and horses. In: *Perspectives in Ethology. Vol. 5* (Ed. by P. G. G. Bateson & P. H. Klopfer), pp. 469–487. New York: Plenum Press.
- Rubenstein, D. I.** 1986. Ecology and sociality in horses and zebras. In: *Ecological Aspects of Social Evolution, Birds and Mammals* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 282–302. Princeton, New Jersey: Princeton University Press.
- Tinbergen, N.** 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, **20**, 410–433.
- Veissier, I., Boissy, A., Nowak, R., Orgeur, P. & Poindron, P.** 1998. Ontogeny of social awareness in domestic herbivores. *Applied Animal Behaviour Science*, **57**, 233–245.
- Wirtz, P.** 1982. Territory holders, satellite males and bachelor males in a high density population of waterbuck (*Kobus ellipsiprymnus*) and their association with conspecifics. *Zeitschrift für Tierpsychologie*, **58**, 277–300.