The Social and Spatial Organisation of Horses.

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It is a captial mistake to theorize before one has data.
Insensibly one begins to twist facts to suit theories;
instead of theories to suit facts.

Sherlock Holmes
in Arthur Conan Doyle's
***A Scandal in Bohemia* (1891).**

Uzrui and me sampling the Black band in late December, 1996.
Thanks to Tarmo Põldmaa for the photograph.

Abstract

A population of feral horses live in the southern Kaimanawa Ranges, New Zealand. These horses live in polygynous social groups with stable membership, called bands. The Kaimanawa horses were the subject of a 3-year field study to describe and examine causes for variation in their behaviour and social and spatial organisation, and to test hypotheses for the origin, operation and persistence of multi-stallion relationships in bands. There were as many mares as stallions in the population. Stallions that were not members of bands lived alone or in unstable bachelor groups. Bands and bachelor males were loyal to home ranges that varied proportionately with the size of the group. Home ranges had central core use areas and overlapped largely or entirely with those of other bands and bachelor males. Groups of horses were selective of habitat and undertook predictable seasonal movements corresponding with changes in climate and the breeding cycle.

Intra- and inter-specific comparison of the behaviour and social and spatial organisation of Equidae showed that species and populations were similar. Differences described from a minority of studies could be attributed to aspects of the studies themselves, particularly poor definition of terms and inadequate empiricism. Sympatric equids adhered to their different social and spatial organisations. "Territoriality" has been a term inappropriately applied in the Equidae. Therefore, adaptive explanations for equid society based on functional relationships with habitat and demography remain unconvincing. Equid phylogeny and close relationships between extant species indicate that phylogenetic inertia may be a better explanation for equid social organisation.

Multi-stallion bands in the polygynous horse pose a challenge to classical ethology in the absence of kin-selected benefits to stallions of sharing a mare group. Previously, Mate Parasitism, By-product Mutualism and Reciprocal Altruism hypotheses have been proposed to explain their existence. However, first, the subordinate stallions were not younger, older or smaller than dominant stallions and contributed more to mare defence than dominant stallions contrary to expectations form the Mate Parasitism hypothesis. Second, multi-stallion bands were not larger or more stable, did not occupy better quality habitat, and had poorer reproductive success than single stallion bands. Moreover, mare reproductive success in multi-stallion bands was poorer than that of single stallion bands and comparable to that of social dispersers. These results are contrary to expectations from the By-product Mutualism hypothesis. Third, dominant stallions did not reciprocate subordinate stallion help in mare defence with tolerance, and subordinate stallions did not improve their access to mares by helping in their defence. Therefore, the Reciprocal Altruism hypothesis was also not supported.

Poorer reproductive success by mares in multi-stallion bands was caused by higher rates of harassment from stallions due to the competitive relationship between stallions. Harassment in multi-stallion bands cost mares in terms of greater displacement, travel and maternal effort, poorer body condition, higher intestinal parasite burdens, lower conception and foaling rates, and greater foetus and foal mortality. The reproductive costs of stallion aggression imposes selection for stable long-term relationships, called consorts, between stallions and mares that facilitate band formation and stability.

The Consort hypothesis proposes that multi-stallion bands are an unselected by-product of consort relationship formation and stallion-stallion dominance behaviour during band formation that occasionally results in multiple stallion-mare consorts. I test for the predictions of the Consort hypothesis with observations of multi-stallion band structure, stallion and mare behaviour, the formation of new single and multi-stallion bands, and an experiment which temporarily removed the subordinate stallion from two multi-stallion bands. Stallion-mare consort relationships were cohesive relationships in bands but stallion-stallion relationships were not. Mares and stallions demonstrated mate recognition and loyalty. Multi-stallion bands formed when more than one stallion had the opportunity to form a consort relationship with a mare during band formation due to changes in stallion dominance. The removal of the subordinate stallion reduced costly mare behaviours proving that relationships between stallion aggression and mare costs were causative and that the different behaviour of stallions and mares in multi-stallion bands were not inherent traits but a response to the multi-stallion social environment. Therefore, the Consort hypothesis was supported in the Kaimanawa feral horse population.

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and critically
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Table of contents

Note on text:

Each chapter is set out in the style of the journal to which it has been submitted. Consequently, there is some repetition, particularly in Methods sections, and there are stylistic differences between chapters. The submitted manuscripts include other authors. For each chapter my input was greatest. I designed the research, undertook the field work, analysed the data and wrote the manuscripts. I was, however, assisted by my co-authors. Kevin Stafford, Ed Minot and Clare Veltman were my PhD supervisors. Elissa Cameron was studying the Kaimanawa horses for her own PhD and thereby contributed to aspects of all manuscripts.