

were always one of the two largest bees.) These data indicate that factors other than body size (e.g. genealogical relationship) may account for worker reproduction in colonies with fewer workers. Because their data from nests with similar worker numbers to mine do not support their conclusions, I fail to understand how they can argue that relative queen size can account for my results. If anything, their results make it unlikely that body size variability is the explanation.

Furthermore, the number of bees in a colony does indeed affect worker reproduction. In colonies with larger numbers of bees, queens cannot dominate worker reproduction as effectively as they can in smaller colonies; that is, workers in larger colonies tend more to display queen-like behaviour and mate (Buckle 1985). My colonies were purposefully kept small and uniform in size in order to control for this effect. The difference between Kukuk & May's four- and eight-bee colonies probably reflects this same phenomenon. Therefore, the results from their eight-bee nests must be considered separately and cannot be generalized to my experiment. As they suggest, the mechanism may be, among other possibilities (Buckle 1985), that a relatively smaller bee occasionally becomes the queen in a larger colony due to the additional influence of bee age on queen determination. Although this phenomenon is non-existent in their four-bee colonies, and uncommon in their eight-bee colonies, they nevertheless argue that it may have occurred in enough of my unrelated colonies that it could explain my results. Based on their own data, I find this argument unlikely.

One last argument against lumping the four- and eight-bee nests together is that the size 'standardization' procedure Kukuk & May have employed is misleading. The 50th size percentile in a four-bee nest means the second largest bee, who must dominate three workers, whereas the 50th percentile in an eight-bee nest means the fourth largest bee, who must dominate seven workers. These dominance situations are certainly not equivalent.

In conclusion, Kukuk & May have used a novel experimental procedure for studying worker reproduction in primitively social bees. These data are interesting in their own right and certainly contribute to our knowledge of the complex relationship between dominance and reproduction in primitively social bees. However, for the reasons outlined above I feel that they do not make a plausible argument against my conclusions.

BRIAN H. SMITH

ARL Division of Neurobiology,  
603 Gould-Simpson Science Building,  
University of Arizona,  
Tucson, AZ 85721, U.S.A.

## References

- Buckle, G. R. 1985. Increased queen-like behaviour of workers in large colonies of the sweat bee *Lasioglossum zephyrum*. *Anim. Behav.*, **33**, 1275–1280.
- Kamm, D. R. 1974. Effects of temperature, day length, and number of adults on the sizes of cells and offspring in a primitively social bee (Hymenoptera: Halictidae). *J. Kans. Entomol. Soc.*, **47**, 8–18.
- Kukuk, P. F. & May, B. P. 1988. Dominance hierarchy in the primitively social bee *Lasioglossum (Dialictus) zephyrum*: is genealogical relationship important? *Anim. Behav.*, **36**, 1848–1850.
- Kumar, S. 1975. Relations among bee size, cell size, and caste, in *Lasioglossum zephyrum* (Hymenoptera, Halictidae). *J. Kans. Entomol. Soc.*, **48**, 374–380.
- Michener, C. D., Brothers, D. J. & Kamm, D. R. 1971. Interactions in colonies of primitively social bees: artificial colonies of *Lasioglossum zephyrum*. *Proc. natn. Acad. Sci. U.S.A.* **68**, 1241–1245.
- Smith, B. H. 1987. Effects of genealogical relationship and colony age on the dominance hierarchy in the primitively eusocial bee *Lasioglossum zephyrum*. *Anim. Behav.*, **35**, 211–217.

(Received 22 April 1988; MS. number: sc-442)

## Contests Between Bands of Feral Horses for Access to Fresh Water: the Resident Wins

When individuals encounter each other frequently, and interact repeatedly, dominance relationships regulate priority of access to critical resources without serious fighting (Wilson 1975). Game theory shows that contests between individuals that have not established dominance relationships can be resolved on the basis of an uncorrelated asymmetry between competitors. On the assumption that residents and intruders might in some cases represent an uncorrelated asymmetry, Maynard Smith (1982) proposed to call this Evolutionarily Stable Strategy the Bourgeois strategy: if resident, escalate until opponent retreats; if intruder, display and retreat if opponent escalates.

For the feral horses inhabiting the sandy islands of the Rachel Carson Estuarine Sanctuary near Beaufort, North Carolina, fresh water is a critical resource, especially during the spring and summer months, when the ambient temperature is high and females are lactating. There are no permanent ponds on the islands, but there are several (8–10) traditional locations where horses can dig to the water table to obtain fresh water. The resulting holes are usually only large enough for one individual at a time to drink. After heavy rains additional fresh water is temporarily available in pools in low-lying wooded areas and bands of horses stop to drink frequently as they move about the island. During periods of low rainfall, however,

pools are absent and several of the traditional locations for digging dry up. Sometimes as few as two locations continue to produce fresh water, and these locations differ from one drought to the next. Bands congregate at the remaining locations for digging and each individual within the band can spend as long as 115 min drinking ( $\bar{X} \pm SD = 19.8 \pm 22.6$  min; median = 14.5 min). Such severe scarcity of water occurs sporadically and lasts only 3–14 days.

Each band consisted of a harem stallion and his harem of one to four females and their offspring (Klingel 1974). Band sizes ranged from three to eight. Half of the 12 bands present on the island during my 3-year study were multi-male bands, which included one to three subordinate stallions in addition to the harem stallion. Breeding records for the last 11 years indicate that subordinate stallions are not offspring of any of the band members (Hoffman 1983; Franke Stevens 1987). These stallions always accompanied the band. Bands were not territorial; all 12 bands ranged over the entire Rachel Carson Estuarine Sanctuary.

Typically, when a band arrived at a water hole the harem stallion was the first to drink followed by the adult females. Once the adult females had drunk, the harem stallion drove them away from the water hole, leaving the juveniles and subordinate stallions to drink. The stallion defended the water hole long enough for him and his harem to drink; a water hole could not be defended continuously unless the band gave up grazing.

When fresh water was in short supply, encounters between bands were frequent, as they competed for access to the few remaining water holes. If a band approached a water hole which was already occupied by another band an agonistic encounter ensued. During 37 h of observation in 1984 and 39 h in 1985, I observed 223 contests between bands at freshwater sources when only two to three locations had fresh water available. The band drinking at the time of the interaction was called the resident band. The band approaching the water was called the intruder band. Contests typically involved only stallions (84% of contests) from the resident and intruder bands. The winner of the interaction was the stallion, resident or intruder, whose band had access to the fresh water immediately following the interaction.

All bands were observed as both residents and intruders. The resident band won 80% (178 of the 223 observed interactions) of these contests at a freshwater source ( $\chi^2 = 79.3$ ,  $df = 1$ ,  $P < 0.001$ ; Table I). Multi-male and single-male bands were equally successful when resident: resident single-male bands won 79% of their contests, and resident multi-male bands won 78% of their interactions

**Table I.** Summary of contests between bands at a freshwater source

	Total (%)
Number of observation hours	76 (100)
Number of contests between bands	223 (100)
Number of contests between bands of equal size	25 (11)
Number of contests won	
By resident band	178 (80)
By intruder	45 (20)
By larger band	137 (61)
Multi-male bands as resident band	
Number of contests	110 (49)
Number of contests won	86 (78)
Number of contests when harem stallion interacts	15 (14)
Number of contests when subordinate male interacts	95 (86)
Single-male bands as resident band	
Number of contests	87 (39)
Number of contests won	69 (79)
Number of contests when harem stallion interacts	78 (90)

( $\chi^2 = 0.20$ ,  $df = 1$ ,  $P > 0.5$ ). When multi-male bands were the resident ( $N = 110$ ; 49% of the contests between bands), the harem stallion interacted with the challenging intruder in only 15 cases (14%), while the subordinate stallion interacted with the intruder in 95 (86%) of the interactions ( $\chi^2 = 55.3$ ,  $df = 1$ ,  $P < 0.001$ ). In contrast, the harem stallion interacted with the intruding stallion in 90% of the 87 interactions when single-male bands were the resident. The only times that neither the harem nor the subordinate stallions of the resident bands interacted occurred when the stallions and their females had left the water hole, leaving only the juveniles behind to fend for themselves. In this situation, juveniles (1–3 years old) were always supplanted by intruding stallions.

Only 61% of the contests were won by the larger band. In contrast to other studies of competition for fresh water (Miller & Denniston 1979; Berger 1981) where a dominance hierarchy according to band size determined the winners of contests, band size was not as important for this population. There was no correlation between band size and the proportion of contests won (Spearman rank correlation coefficient  $r_s = 0.41$ ,  $N = 12$ ,  $P > 0.05$ ), but there was a significant correlation between the proportion of contests as resident and the proportion of contests won ( $r_s = 0.96$ ,  $N = 12$ ,  $P < 0.01$ ). When bands of equal size contested access to the

water ( $N=25$ ) the resident won 80% of the contests.

The assumptions for the bourgeois strategy to be evolutionarily stable are met (Maynard Smith & Parker 1976; Maynard Smith 1982). Since water is defended only temporarily, in any encounter each band has an equal chance of being resident at the water. The payoff from access to fresh water is also presumably nearly the same for any band: all bands are in the same habitat and experience the same heat stress. Resource holding potential of the stallions depends on their fighting ability. Since males are about the same size, evaluation of fighting ability cannot easily be based on size. Furthermore, since stallions in different bands rarely fight, any male is likely to face uncertainty about the fighting ability of other stallions. Slight differences in resource holding potential should not alter the outcome of a contest determined by an ownership asymmetry (Parker 1974; Hammerstein 1981). Only when the intruder has a substantial, detectable superiority in fighting ability should he escalate (Hammerstein 1981). Escalated fights in horses often lead to severe leg injuries (Berger 1981), and lame stallions run the risk of losing their mares. This risk is clearly greater than the cost of waiting until the resident band finishes drinking. Contestants at water holes clearly have accurate information about which is the owner and which is the intruder.

Thus, the conditions for an evolutionarily stable ownership convention are satisfied in this case. Most of the contests (80%) are settled by the ownership asymmetry. If periods of water shortage occurred more often, so that bands interacted with each other more frequently, we might expect that dominance relationships would govern access to water. Instead, contests between bands over water are settled by a rule based on an uncorrelated asymmetry: ignore small differences in resource holding potential and respect ownership.

I am grateful to R. H. Wiley for his intellectual support throughout this study, and to E. E. Stevens, P. H. Klopfer, H. C. Mueller and P. Kappeler for constructive comments on this manuscript.

ELIZABETH FRANKE STEVENS

*Department of Biology,  
The University of North Carolina,  
Chapel Hill, N.C. 27514, U.S.A.*

Present address: National Zoological Park, Smithsonian Institution, Washington, D.C. 20008, U.S.A.

## References

Berger, J. 1981. The role of risks in mammalian combat:

- zebra and onager fights. *Z. Tierpsychol.*, **56**, 297–304.
- Franke Stevens, E. 1987. Ecological and demographic influences on social behavior, harem stability, and male reproductive success in feral horses (*Equus caballus*). Ph.D. thesis, University of North Carolina at Chapel Hill.
- Hammerstein, P. 1981. The role of asymmetries in animal contests. *Anim. Behav.*, **29**, 193–205.
- Hoffman, R. 1983. The development of social behaviour in immature males of a feral horse population (*Equus caballus*). Ph.D. thesis, Universität Tübingen, West Germany.
- Klingel, H. 1974. A comparison of the social behaviour of the Equidae. In: *The Behaviour of Ungulates and its Relation to Management* (Ed. by V. Geist & F. Walther), pp. 124–132. Morges, Switzerland: International Union for Conservation of Nature and Natural Resources.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Maynard Smith, J. & Parker, G. A. 1976. The logic of asymmetric contests. *Anim. Behav.*, **24**, 159–175.
- Miller, R. & Denniston, R. H. 1979. Interband dominance in feral horses. *Z. Tierpsychol.*, **51**, 41–47.
- Parker, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. *J. theor. Biol.*, **47**, 223–243.
- Wilson, E. O. 1975. *Sociobiology*. Cambridge, Massachusetts: Belknap Press.

(Received 21 January 1988; revised 6 April 1988;  
MS. number: AS-519)

## Extra-pair Courtship, Copulation and Mate Guarding in Wild Zebra Finches *Taeniopygia guttata*

Extra-pair copulation occurs regularly in many monogamous bird species and males minimize the risk of cuckoldry in one of two main ways: frequent pair copulation or mate guarding by close following (Birkhead et al. 1987). The aim of this study was to examine extra-pair activities and paternity guards in wild zebra finches in the field; the study was undertaken to complement a detailed investigation of sperm competition and associated behaviour in captive, domesticated zebra finches (Birkhead et al. 1988).

The study was conducted at a colony of 20–40 pairs of zebra finches near Wunghnu (36°00'S, 14°24'E), northern Victoria, Australia, during January and early February 1988. Most birds had been individually colour-ringed prior to the study and the identities of all breeding zebra finches were determined from weekly nest inspections (see also Zann & Straw 1984). Four pairs of zebra finches were observed in detail through the pre-laying, egg-laying and early incubation periods (mainly from day –5 to day +4, where day 0 = the day the first egg of a clutch is laid). A total of 135 nest-hours of