DAYTIME BEHAVIOUR OF THE GREY-HEADED FLYING FOX PTEROPUS POLIOCEPHALUS TEMMINCK (PTEROPODIDAE: MEGACHIROPTERA) AT AN AUTUMN/WINTER ROOST

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The grey-headed flying fox (Pteropus poliocephalus Temminck) is a threatened large fruit bat endemic to Australia. It roosts in large colonies in rainforest patches, mangroves, open forest, riparian woodland and, as native habitat is reduced, increasingly in vegetation within urban environments. The general biology, ecology and behaviour of this bat remain largely unknown, which makes it difficult to effectively monitor, protect and manage this species. The current study provides baseline information on the daytime behaviour of P. poliocephalus in an autumn/winter roost in urban Sydney, Australia, between April and August 2003. The most common daytime behaviours expressed by the flying foxes were sleeping (most common), grooming, mating/courtship, and wing spreading (least common). Behaviours differed significantly between times of day and seasons (autumn and winter). Active behaviours (i.e., grooming, mating/courtship, wing spreading) occurred mainly in the morning, while sleeping predominated in the afternoon. Mating/courtship and wing spreading were significantly higher in April (reproductive period) than in winter (non-reproductive period). Grooming was the only behaviour that showed no significant variation between sample periods. These results provide important baseline data for future comparative studies on the behaviours of flying foxes from urban and 'natural' camps, and the development of management strategies for this species.

Key words: flying fox, Pteropus poliocephalus, diurnal behaviour, bat colony, winter roost.

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PTEROPUS poliocephalus (Megachiroptera) is one of the largest bat species in the world, weighing between 600 and 1000 g (Hall and Richards 2000). This species is distributed along the eastern coast of Australia and ranges from Melbourne, Victoria, to Miriam Vale, Queensland (Hall and Richards 2000). P. poliocephalus is phytophagous and feeds preferentially on nectar and pollen of eucalypts (Parry-Jones and Augee 1991; Eby 1995). They are social animals and roost in large aggregations called 'camps' in rainforest patches, mangroves, open forest and riparian woodland (Ratcliffe 1932; Nelson 1965).

Many flying fox species are in decline worldwide (Fujita and Tuttle 1991). Often difficulties exist in developing appropriate management strategies for flying foxes, because there is generally very little known about their biology (e.g., Reardon 1999). Loss of habitat and landscape alteration has impacted significantly on this species. In May 2001, P. poliocephalus was listed as 'Vulnerable' in New South Wales under the Threatened Species Conservation Act 1995 (Eby and Lunney 2002). Potentially available feeding and roosting habitat for this species is limited (Duncan et al. 1999) and many flying fox colonies are located either in remnant forest or, increasingly, in urbanised areas (Birt et al. 1998). Occupation of urban areas is a direct result of habitat loss and clearing, and consequently the length of time urban camps are occupied is currently being extended, with some colonies occupied over the whole year (Puddicombe 1981; Parry-Jones and Augee 2001).

Flying foxes are an ecologically important species necessary for the maintenance of forest ecosystems through their activities in pollinating and dispersing seeds over long distances (Fleming and Heithaus 1981; Marshall 1983; Eby 1995). As such there is a need to conserve these animals. Currently limited information exists on the behaviour of P. poliocephalus and there is no general method for evaluating the behaviour of this threatened species. This confounds efforts to both manage and conserve

P. poliocephalus. The behaviour of flying foxes in general has been studied inadequately and there is little known about long-term behavioural patterns in many species (Funakoshi et al. 1991; Courts 1996). The most detailed studies on wild populations of flying foxes have been conducted by Nelson (1965, for P. poliocephalus), Neuweiler (1969, for P. giganteus), and Markus (2002) and Markus and Blackshaw (2002, for P. alecto). The behaviour of P. poliocephalus was first studied in wild populations by Ratcliffe (1932). Ratcliffe's (1932) and Nelson's (1965) studies focused on flying fox colonies in a variety of environments. In a more recent study, Puddicombe (1981) investigated the behaviour of P. poliocephalus in a colony in Sydney. This study had the disadvantage that only a small number of bats of known sex and age were studied to assess different behaviour types. Puddicombe's (1981) research represents the only previous quantitative study of P. poliocephalus behaviour. Other behavioural studies on pteropid species have been performed outside of Australia, however, most took place in captive environments (Carroll 1979; Advani 1982; West and Redshaw 1987; Young and Carroll 1989; Funakoshi et al. 1991; Courts 1996).

Many social behaviours among flying foxes exhibit seasonal patterns, with the majority of behaviours expressed while flying foxes occupy summer camps between the birthing period and the following mating season (Nelson 1965; Markus 2002). After this time, flying foxes traditionally leave summer roosts to form smaller winter colonies (Nelson 1965). Currently, little is known about the behaviour of P. poliocephalus during autumn and winter. The purpose of this study was to quantify directly the daytime behaviours of P. poliocephalus at an autumn/winter roost site. As urbanisation of habitat surrounding roosting areas has generally increased, changes in behavioural patterns may be occurring. It is essential that knowledge is gained about the behaviour of P. policephalus so that effective management of this species can occur. Therefore, we assessed a number of simple behavioural categories among a group of individuals to determine general behavioural patterns. These were examined within the context of creating an effective procedure to assess behaviour so that in future comparative studies can take place.

MATERIALS AND METHODS

Study site

The study was performed on bats of the flying fox colony at the Cabramatta Creek Flying Fox Reserve, Warwick Farm, western Sydney (33°55'S; 151°00'E) between 15 April and 2 August 2003. The reserve is surrounded on three sides by Cabramatta Creek and covers an area of 2.22 ha. Between 5,000 and 30,000 bats inhabit this site, and population estimates are increasing (Newman 1996). The colony is comprised predominantly of polygamous groups, monogamous pairs and juvenile groups. Although generally there is a decrease in the number of individuals occupying the site during autumn and winter, the reserve is regularly occupied throughout the year (Newman 1996), providing the opportunity to perform behavioral studies during autumn and winter.

Data collection

The behaviour of roosting flying foxes was recorded once per 10-day sampling period between 15 April and 2 August 2003 (i.e., two to three 7 hour recording days per month). The total observation time was 147 hours for the whole study period. The following behaviours were recorded:

(a) sleeping: eyes closed and wings wrapped around body.

(b) grooming: licking and scratching body and/or head.

(c) mating/courtship: males licking and/or copulating with female.

(d) wing spreading: wings wide open, extended on side or in front of body.

(e) movement in tree: climbing along branch or trunk.

(f) flight: within tree or out of and into tree.

(g) wing flapping: fanning body with wing(s).

(h) aggression: fighting between individuals, which was not directly related to mating or courtship.

(i) nursing/maternal behaviour: juvenile attached / nursing.

Observations started approximately 10 to 15 min after the arrival of the observer at the observation point at 0930 hours and ended at 1720 hours. The bats settled after approximately 5 min after the observer's arrival and showed no apparent response to the observer. As it is impossible to record the behaviours of all bats of a colony concurrently, a number of bats in the colony were randomly selected for instantaneous time sampling (Altmann 1975; Kunz 1988). Observations were conducted on groups of bats (average ± SE number of individuals per sampling session = 32.53 ± 0.47) roosting in adjacent branches containing adults of both sexes in 10 min intervals. The bats' behaviour was observed directly using 10 x 40 binoculars (Zeiss, Germany) (see Erkert 1982). During each 10 min observation period, the number and sex of bats performing any of the above listed behaviours was recorded. No observations were conducted during continuous rain, as the bats' bodies were enclosed within their wings

and all active behaviours ceased. The behaviours of bats on surrounding trees were routinely checked to ensure that the behaviours of the sampled bats corresponded to those of the bats in other parts of the colony. The level of sunlight on the tree was recorded and graded on a scale of 0 to 8 (with 0 = no cloud cover, sunny, and 8 = completely overcast). While occasional disturbances occurred at the site during observations, they were very rare and were disregarded in the analysis.

Statistical analysis

Percentages of the number of bats observed performing each behavioural category were calculated and grouped into one-hour blocks. The four most frequently occurring behaviours (sleeping, grooming, mating/courtship, wing spreading) were analysed to determine whether behaviours differed between time of day and the sample periods using a two-factor repeated-measures ANOVA (SYSTAT, Version 9, SPSS Inc., 1999). Although nursing and maternal behaviour was the second most frequent active behaviour, it was not analysed due to its rare occurrence after the first two sample periods. All other behaviours (i.e., movement in tree, wing flapping, aggression) were also not statistically analysed due to their relatively rare occurrence.

Raw data were analysed as no transformations improved the normality or homogeneity of variance of the data. A linear regression was performed to examine the relationship between sunlight and each behaviour type analyzed. There were no relationships between sunlight and behaviour type (R^2 = 0.001 to 0.007). As the majority of days were dry and sunny, the effect that sunlight had on activity was generally a correlate of time of day. Therefore, sunlight levels were excluded from further analyses. While significant results need to be treated with caution as statistically their occurrence may be due to heteroscedasticity in the data, the patterns were of sufficient strength and appeared, based on empirical observations, to be biologically significant.

RESULTS

While P. poliocephalus is considered to be a nocturnal species (Hall and Richards 2000) and spends most of the day asleep, animals exhibited short bouts of irregular activity throughout the day. On average 83% of all bats were asleep during the daytime, while only 17% were engaged in active behaviours. However, there were a number of significant differences observed between the different times of day and sample periods for the behaviours examined.

Sleeping

Sleeping patterns in P. poliocephalus varied significantly throughout the observation period (F = 1.927, p = 0.040, repeated measures ANOVA). The lowest percentage of sleeping bats was recorded in mid April (Fig. 1a). From then onwards, an increased number of bats were asleep during the day, with peaks between 5 May and 3 June and between 24 June and 13 July, and a lull between 4 and 23 June 2003 (Fig. 1a). There was a significant difference in the percentage of bats asleep throughout the day (F = 22.267 p = 0.000, repeated measures ANOVA). Sleeping was least common between 0930 and 1020 hours (0.70 ± 0.03) and most common between 1530 and 1720 hours (0.92 ± 0.02) (Fig. 1b).

Grooming

Grooming was a common behaviour and accounted for 41 ± 0.39% of all active behaviours recorded. The percentages of grooming bats remained fairly constant between April and August and there were no significant differences between sample periods (F = 0.835, p = 0.595, repeated measures ANOVA). Grooming activity changed significantly throughout the day (F = 11.292, p = 0.002, repeated measures ANOVA) (Fig. 2), and was most pronounced between 0930 and 1420 hours. After this time, grooming steadily dropped to an overall low between 1630 and 1720 hours.

Mating and courtship

Mating and/or courtship activities (9.5 ± 0.14% of all active behaviours) differed significantly between sample periods (F = 4.315, p = 0.000, repeated measures ANOVA) (Fig. 3a). The highest percentage of individuals engaged in mating and courtship occurred during April. From then on, this behaviour steadily decreased until early June. Between 4 June and 3 July 2003 mating increased again, before reaching an overall low between 24 July and 2 August 2003. Reproductive behaviours varied significantly during the day, with significantly more mating and courtship occurring in the morning than in the afternoon (F = 27.125, p = 0.000, repeated measures ANOVA) (Fig. 3b). Mating and courting activities decreased consistently throughout the day reaching lowest levels between 1630 and 1720 hours.

Wing spreading

Wing spreading accounted for 13 ± 0.17% of all active behaviours. There was a significant difference in the percentage of individuals with spread wings between sample periods (F = 2.716, p = 0.003, repeated measures ANOVA) (Fig. 4a). Wing

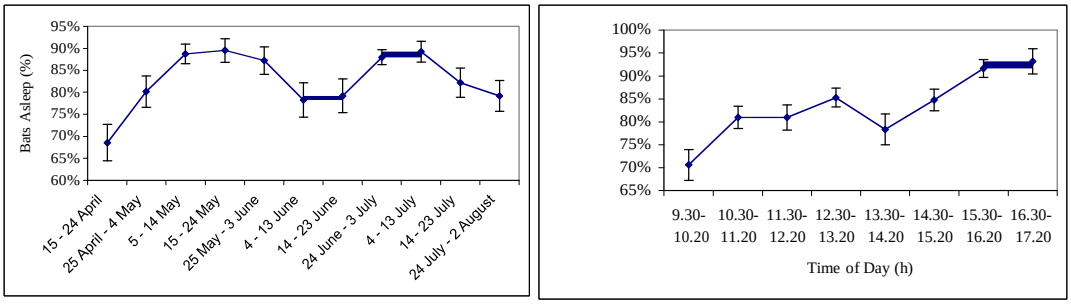

Fig. 1. Bats asleep (%) between (a) 15 April and 2 August 2003, and (b) 0930 and 1720 hours. Standard errors (SE) are indicated by error bars.

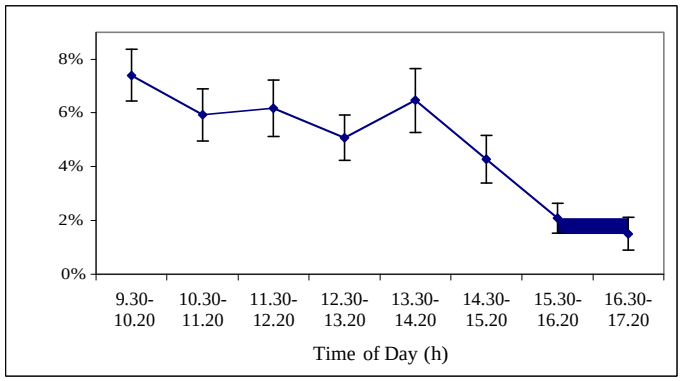

Fig. 2. Bats grooming (%) between 0930 to 1720 hours. Standard errors (SE) are indicated by error bars.

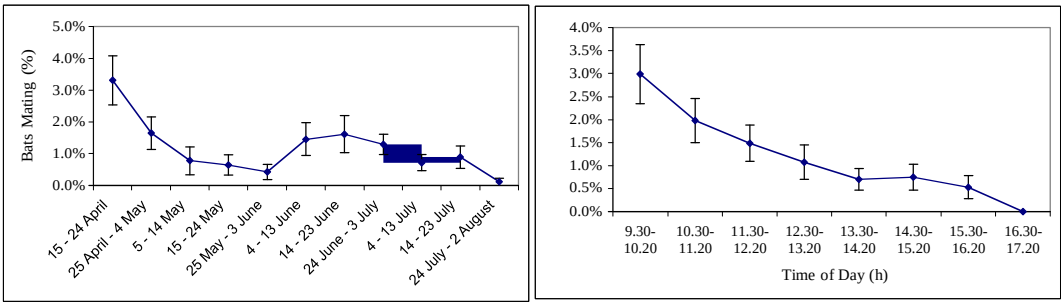

Fig. 3. Bats mating/courting (%) between (a) 15 April and 2 August 2003, and (b) 0930 and 1720 hours. Standard errors (SE) are indicated by error bars.

spreading was most common between April and early May, and mid July to early August, and least common between early May and mid July (Fig. 4a). The percentage of bats with spread wings differed significantly with time of day ($F = 7.132$, $p = 0.011$, repeated measures ANOVA) (Fig. 4b). The highest percentages of bats with spread wings occurred between 0930 and 1220 hours. From then onwards, the percentage of bats with spread wings decreased steadily reaching an overall low between 1630 and 1720 hours. 88% of all bats displaying spread wings were males.

DISCUSSION

Sleeping

Sleeping was the most common behaviour in P. poliocephalus. The lowest percentage of individuals asleep during the day occurred during mid-April. April is the month in which conception occurs and is in the middle of the breeding period (Puddicombe 1981; Eby 1995), when individuals would presumably be more active. Sleeping occurred most frequently during May and July. Funakoshi et al. (1991) observed that sleeping durations are closely

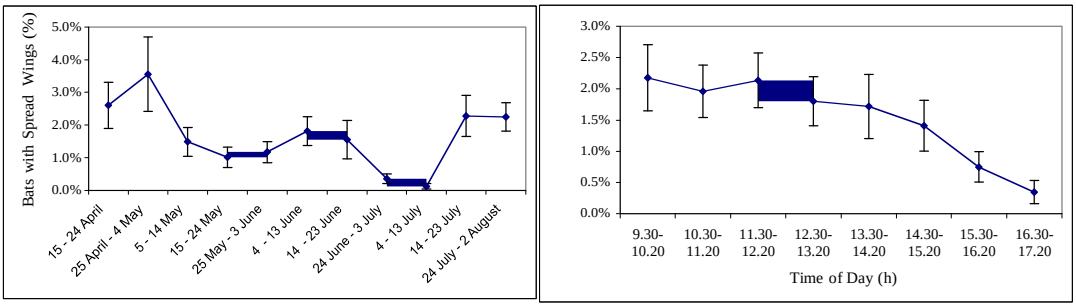

Fig. 4. Bats with spread wings (%) between (a) 15 April and 2 August 2003, and (b) 0930 and 1720 hours. Standard errors (SE) are indicated by error bars.

linked with ambient temperatures in P. dasymallus, and detected a positive relationship between low temperatures and a decrease in activity levels, which may explain why sleeping was more common during these colder months. However, there was a decline in the percentage of sleeping bats in June and towards the end of July. During this time the ratio of females to males at the colony was significantly lower than during other times (Connell unpubl. data). At present we do not know whether this could have influenced the sleeping behaviour of the bats. Consequently, it remains uncertain why the bats slept less during these times.

The percentage of bats asleep changed significantly throughout the day. In general, sleep occurred predominantly in the middle of the day and late afternoon, between 1630 and 1720 hours. The high percentage of sleeping bats late in the day may indicate that bats are sleeping to save energy before the fly-out in the evening. In general, there is little known about the sleeping behaviour of P. poliocephalus. The only previous study on the sleeping behaviour of this species was conducted by Puddicombe (1981). He reported that P. poliocephalus was awake for the majority of the day, except during the early morning (0630 to 0800 hours; this time period was not included in our study) and late afternoon (1600 to 1730 hours), when sleep primarily occurred. Our current findings only partially concur with Puddicombe's (1981) results. We also observed increased sleeping in the late afternoon, but did not find the majority of the bats awake during the day. The reason for this discrepancy is not clear. Other investigations on the sleeping behaviour of other pteropodids (Bradbury 1977; Carroll 1979; Young and Carroll 1989; Funakoshi et al. 1991) suggest that daytime activity levels in the roost are usually low and that the bats spent the majority of the day asleep.

Grooming

Grooming was the second most common behaviour observed in this study. This behaviour did not change significantly during the observation period. This may indicate that grooming is a behaviour that is not affected by season, and is required at similar intensities at all times of year. Nelson (1965) observed that P. poliocephalus regularly groomed fur and wing membranes for several hours per day in order to maintain clean wing membranes and to reduce oily secretions from epithelial glands. It may also help in the development of social bonds and may be part of the pre-copulatory behaviour of males (Nelson 1965). However, comparisons cannot be made as there was no quantitative assessment of grooming in Nelson's (1965) study.

There was a significant difference in grooming activity throughout the day. Bats groomed more frequently in the first half of the day until 1530 hours when a significant decline in grooming occurred. Puddicombe (1981) investigated grooming by recording both wing and body licking in P. poliocephalus. While there was no statistical analysis of grooming, the data indicate that the two behaviours occurred more frequently in the morning, corresponding with the results of our study. Similar grooming patterns have been observed in other species of bat. Burnett and August (1981) found that Myotis lucifugus mainly groomed in the morning, after the return from their feeding sites and again prior to their nightly departure. We also recorded higher levels of grooming in P. poliocephalus in the morning, but were not able to accurately quantify grooming levels late in the day due to poor visibility. However, limited observations of the bats from the Cabramatta site indicate increased grooming prior to the evening fly-out.

Mating and courtship

Mating and courtship behaviours differed significantly amongst sample periods, with highest levels recorded in April, after which it decreased consistently until early June. This was an expected result as the breeding season of P. poliocephalus peaks between March and May (Puddicombe 1981; Eby 1995). Surprisingly, there was an increase in the percentage of bats mating during June, followed by an overall low in early August. Despite the fact that Nelson (1965) observed that P. poliocephalus males attempted to copulate with females all year, the increased matings during June observed in our work were unexpected for two reasons. Firstly, the ratio of females to males had reached an overall low during this time (Connell, unpubl. data), and secondly, these matings occurred at the end of the reproductive period, when males usually have smaller testicular volume (McGuckin and Blackshaw 1992) and consequently mate less frequently at this time (Puddicombe 1981; Eby 1995). However, since there are no other detailed studies on this species available to either confirm or contradict our results, we cannot disregard our findings. Until such studies become available, it is unclear whether the increased matings in June are part of the natural reproductive behaviour of P. poliocephalus or are due to other factors.

The extent of courtship and mating of P. poliocephalus changed during the day. Highest percentages of courting and mating bats were observed in the morning, after which this behaviour declined steadily reaching lowest levels in the late afternoon. There is very little information available on diurnal changes in mating activity for this species. Puddicombe (1981) noted two instances in the mid-afternoon where a copulation attempt and pre-copulatory licking occurred over a two-day period. However, the time frame of this study was so brief, that no comparisons can be made. Daily reproductive and mating patterns have been investigated in captive P. rodricensis (Carroll 1979; Young and Carroll 1989); however these studies took place during artificial periods of darkness, rendering them unsuitable for comparisons between the two species.

Wing spreading

Wing spreading was mainly performed by male bats (88% of all observations). There may be a relationship between wing spreading and aggression as this behaviour occurred more frequently when the bats were exhibiting peak levels of mating and courtship behaviours (Figs 4a,b). This may indicate that bats with spread wings are protecting territories or making threat displays to other bats and/or indicating the individual's social status. However, increased levels of wing spreading were also recorded outside the breeding period (last two sample periods in July). Currently, there is no literature available on wing spreading and its function in P. poliocephalus. Puddicombe (1981) recorded wing positions, but classified positions as closed or hanging at the sides of the bats' body, and described a behaviour he classified as 'wing spread alarm', which occurred when animals were startled. However, in Puddicombe's (1981) study, bats apparently opened their wings only briefly and not to the full extent. Wing-displays have been recorded in P. alecto and were used as a threatening display between resident and intruding males (Markus 2002). Carroll (1979) recorded the 'wing shake' in P. rodricensis. The wing shake was classified as an aggressive behaviour, which is exhibited by both sexes in which the wings are stretched out in front of the body. However, the wing spread which was recorded in the present study encompassed postures in which the wings were outstretched along the sides of the body. The differences in wing postures may be indicative of differences between species or alternatively between recording techniques. Further investigations are needed to fully understand wing spreading and its function in flying foxes.

Other behaviours

There were a number of other behaviours observed in the bats. However, they were not statistically analyzed because they occurred rarely or not at all during certain sampling periods. Wing flapping (4.0 ± 0.14% of all active behaviours) was recorded frequently during the first two sample periods, especially during periods of higher temperatures and strong sunlight. This supports the hypothesis that wing flapping has a thermoregulatory function (Nelson 1965; Puddicombe 1981).

Daytime flights (4.1 ± 0.06% of all active behaviours) and movements in the tree (7 ± 0.09%) were, as in other bats (Carroll 1979; Burnett and August 1981; Funakoshi et al. 1991), a rare event in P. poliocephalus, and were mainly caused by changes in roosting positions in response to conspecifics, retreat from sunlight or ground disturbances. Agonistic behaviour was rarely exhibited, and accounted for 2.4 ± 0.07% of all active behaviours recorded. This coincides with observations from Puddicombe (1981), who also noted that aggressive interactions were reduced during winter. In general, we observed little physical contact between the bats. The most intense physical contact was between females and their young (19 ± 0.25% of all active behaviours) (see also Ratcliffe 1932; Nelson 1965; West and Redshaw 1987) during April and early May. After May nursing or other maternal behaviours were rarely observed.

Conclusion

While we are not able to explain all behaviours we recorded in P. poliocephalus, our study provides baseline information on the behaviour of this species for further investigations. The 10 min time sampling regime we had chosen for our study appeared adequate for recording flying fox behaviours and may be suitable for future comparative studies of this species. It is important to obtain baseline information about a species' behaviour as it can indicate the relative fitness of the colony. With the reduction of roosting and feeding habitat available in eastern Australia, many flying foxes are forced to occupy new site locations and/or utilise sites in different ways. This may have an effect on the behaviour of the animals occupying these colonies as competition for resources is increased. Future studies, which may facilitate effective management of P. poliocephalus, include concurrent investigations of behaviour in colonies located in urban and natural environments to determine if differences in behaviours are expressed, and long-term monitoring of behaviour of flying foxes. For effective management of this species to occur, fundamental information about its behaviour is essential.

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