## Title
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# BOXING IN RED KANGAROOS, *MACROPUS RUFUS*: AGGRESSION OR PLAY?

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ABSTRACT: Fighting in a boxing style is the most spectacular behaviour of red kangaroos, *Macropus rufus*, yet its structure and function have not been analysed in detail. Patterns of sparring, kicking and wrestling occur between mothers and young (especially males), in formalized contests between males, and in escalated conflicts over resources (shelter, water, oestrous females). Observations were made of fighting behaviour in free-living and captive individuals. The frequency of fighting between various age/sex classes in the field was determined and the structure of fighting over a water resource was analysed from a 12 h videotape record. These results were compared with an analysis of 85 videotaped plus 35 other fights observed in a captive group of eight males (age 1 - 7 year). These fights were formalized contests which did not involve or resolve any immediate conflict over a resource. Such fights share many of the properties ascribed to play-fighting. They are initiated with invitational behaviour that does not include characteristic threat behaviour seen in fights over a resource. They involve self-handicapping, some lack of dominance distinctions, and usually several bouts occur interrupted by mutual pauses. The structure of the fight suggests that the main goal is to push or wrestle the opponent off balance and down to the ground rather than inflict potentially injurious kicks as seen in resource conflicts. Furthermore larger opponents often adopt an inferior flat-footed stance and dominants and/or winners kick significantly less than losers. The context, goals and structure of these non-resource based fights suggest that they are a form of play-fighting. Selection of play partners on the basis of size/dominance or kinship indicate that such play-fighting in red kangaroos is neither truly cooperative nor disruptive and selfish. The behaviour most likely functions as a form of non-damaging assessment of opponents with benefits in skill development in younger individuals.

The red kangaroo *Macropus rufus* is a large grazing macropodid from the inland plains of the Australian arid zone. Males may attain body weights of 90 kg or more but females rarely exceed 35 kg. The mating system is one of hierarchical promiscuity (after Wittenberger, 1979), male competition for mates is intense and usually the largest male gains an exclusive consort relationship with an oestrous female (Croft, 1981). Popular mythology of kangaroo behaviour (e.g. Williamson, 1978) would have it that a rival's disembowelment and death is a frequent consequence of male fights. However, death as a

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result of fighting has only been documented in captivity (Sharman & Calaby, 1964). As in other animal species, fatal wounding is by no means a common result of such fights.

In red kangaroos, fighting occurs in two main contexts: (1) conflict between two or more individuals in disputed access to a resource, whether a shelter site, water or (for males) an oestrous female; and (2) circumstances where no resource is in immediate dispute (Croft, 1981). Resource-related and resource-unrelated fighting may indicate behaviour in red kangaroos that is analogous to 'serious' and 'play-fighting' (Fagen, 1981; Hole & Einon, 1984), respectively, in other mammal species. Play is a common phenomenon in endothermic vertebrates (Fagen, 1981) and play-fighting is typical of sexually dimorphic species (Symons, 1978). However, a satisfactory definition of play has proved vexing (Martin, 1984) and it is usually identified as behaviour which lacks an obvious goal and is therefore not immediately concerned with the participants' current survival, occurs in specific contexts, and may include unique play signals (Hole & Einon, 1984). Play and non-play are usually distinguished from their structure (Henry & Herrero, 1984; Owens, 1975; Bekoff, 1978) and so an operational definition of play is often employed.

Behaviour such as play-fighting may use motor patterns that mimic those used in competitive fighting for a limited resource. This makes the discrimination of serious fighting from play-fighting difficult. However, play patterns may be incomplete, inhibited, exaggerated or uneconomical, repetitive, sequentially unordered or re-ordered, causally distinct and even unique to the play context (Fagen, 1981). Pellis and Pellis (1987) argue that only the last of these criteria unambiguously distinguishes play and that few, if any, studies have successfully defined play by the other structural criteria listed. Pellis (1988) promotes an analysis of the targets attacked and defended in play-fighting and serious fighting as an objective measure of the differences between the two behaviour categories. Apart from potential differences in structure, the selection of partners may differ between play and non-play contexts. For example, smaller individuals may actively avoid agonistic interactions with larger ones but engage them in play-fighting since play may serve one or more of several functions—motor or cognitive training (Bekoff & Byers, 1981), regulation of developmental rates (Fagen, 1981) and socialisation (Poirier & Smith, 1974)—where interaction with a larger individual is of benefit. However, like the defining characteristics of play, functional hypotheses about this behaviour are contentious (Martin, 1984; Hole, 1988).

This study examines the structure of fighting behaviour in red kangaroos in both resource-related and resource-unrelated contexts to determine if the behaviour performed when resources are not in con-
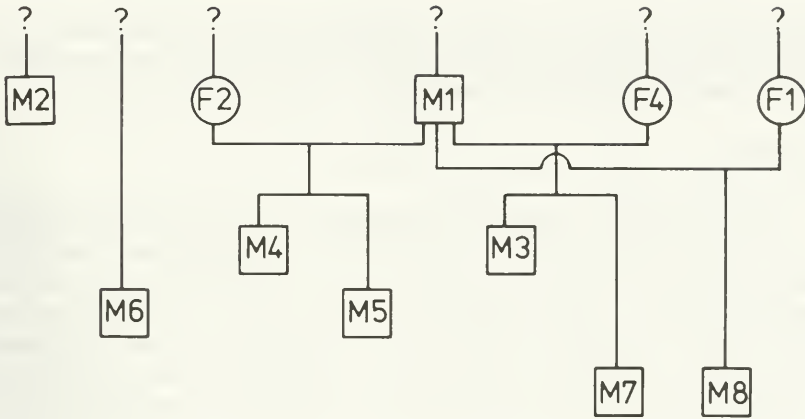
**FIGURE 1.** Pedigree of eight males observed in captive group (M = Male, F = Female).

tention is play-fighting. Data are drawn from both field and captive populations. Fighting partner selection is examined in the captive population to further identify play-fighting and its possible function.

## MATERIALS AND METHODS

*Animals*

Data on fighting behaviour were collected from free-ranging red kangaroos at Fowlers Gap Arid Zone Research Station, 110 km north of Broken Hill, in north-western New South Wales and from a captive colony, derived from the Fowlers Gap population, and held at Cowan Field Station on the outskirts of Sydney, Australia. The field site is described in detail in Croft (1981).

The captive colony initially contained 15 individuals (6 M and 5 F adults, 2 M sub-adults, 1 M and 1 F juveniles). Three young emerged from the pouch and one female and her young died by the end of the study. All individuals were identifiable from size and colour differences, characteristic markings and/or coded ear marks. The adult females ranged in age from 3.5 to 8.5 year and three had young-at-foot (1 M, 2 F). The study focussed on the adult and sub-adult males, hereafter referred to as: M1 (5 year), M2 (6.5 year), M3 (3.5 year), M4 (3.5 year), M5 (2 year), M6 (2 year), M7 (1.5 year), M8 (1.5 year). The male pedigree is shown in Figure 1. The colony was housed in one of three yards (approximately 30 m x 40 m), each surrounded by a 2 m wire-mesh fence. Some rotation of the colony between these yards was necessary to maintain a grass cover for the duration of the

study. Each yard had a shelter, a self-filling water trough, and a food shed which supplied *ad libitum* pelleted food supplements. Neither food, water, or shelter was limiting.

*Procedure*

Two categories of fighting behaviour were distinguished based on their context: resource-related (RR) and resource-unrelated (RU) fighting. Results on rates and durations of RU fighting in various age/sex classes of free-ranging kangaroos were derived from unpublished data collected on the social behaviour of red kangaroos. This study is described in Croft (1981). The data set comprised 1500 h of focal-animal sampling of the various age/sex classes during the diurnal period.

Results on RR fighting behaviour resulting from competition for a water resource were derived from unpublished data collected during a study described in Croft (1985). A 12 h videotape record of agonistic behaviour between red kangaroos at a water trough in mid-summer was used. This record was collected from 2000 - 2400 h using a Sony Portapak VCR and Sony camera attached to a Javelin night vision device. Observations were made from a hide located 35 m from the trough and the trough was illuminated with dim red light.

For the captive study, observations were made from a small, elevated hide set up along one of the fences in a position that offered an unobstructed view of all animals. Observations, totalling 100 h, were made twice weekly for periods of 3 h around dusk and the following dawn of two consecutive days for six months (March - August). Nighttime observations were made under red-filtered lights. All male-male fights (and 'fights' involving females, usually mother-young interactions) were recorded using a Sony Portapak VCR and camera. A more complete record of each male's social behaviour was obtained by focal sampling each male for a half-hour period, recording all its social interactions on audiotape. The order of these focal watches was rotated so that each male was observed over the range of different times within observation periods. Interactions were defined as being non-agonistic, agonistic, or sexual after Croft (1981). The initiator of each interaction was noted and, for agonistic interactions, the 'winner' or 'loser' identified. The outcome of agonistic interactions where one individual supplanted another (i.e., exclusive of fights) was used to define a male dominance hierarchy using the methods of Russell (1970).

The incidence of RR fights in the captive group was rare ( < 1% fights) and so further analysis was confined to RU fights. The videotapes of RU fights were analysed in slow motion (0.22 of real time). Every action of the combatants was recorded in the sequence it occurred on a Datamyte 904 event recorder allowing resolution of be-

## TABLE 1
### Frequency of Fights and Mean and Range of Fighting Bouts between Various Size/Sex Classes of Red Kangaroos in the Field

| Dyad | Frequency per 100h (n) | Mean bouts per fight (range) |
|---|---|---|
| Male large - Male large | 3.5 (3) | 1.3 (1-2) |
| Male large - Male medium | 2.6 (5) | 2.8 (1-6) |
| Male medium - Male medium | 5.1 (30) | 5.1 (1-16) |
| Female - Female | 0.3 (2) | 1.0 (1-1) |
| Male young - Mother | 9.0 (8) | 1.6 (1-4) |
| Female young - Mother | 4.8 (4) | 1.3 (1-4) |

havioural durations to 0.01 min. The Datamyte record was transmitted to an Apple II computer for further analysis of the frequency, duration, and transition frequency of each behaviour. The following behaviour units were used (see also Croft, 1981): approach ( > 1 m to < 1 m), mutual nose sniffing, sniffing another body part of opponent, face (head oriented towards opponent), face away (head oriented away from opponent), stiff-legged walk (individual walks slowly on tips of toes with back arched accentuating body size), upright stance (standing flat-footed with back vertical), high standing (standing on tips of toes and tail, fully extended vertically), forearms locked (both forearms out-stretched and holding opponent's arms), head arch (head tilted back, nose upwards, throat exposed to opponent), pawing (raking body surface of opponent with both forepaws), hit (striking opponent with one forepaw), push (forcing opponent backwards), push down (forcing opponent towards the ground), push away (forcing opponent to disengage), kick (striking opponent with both hindfeet while balanced on tail), allogrooming, selfgrooming (with body part groomed/scratched), mouthing (nibbling head region of opponent), licking forearms, pause (both individuals standing apart on forepaws and hindfeet), move away slowly (walk), move away rapidly (hop), simultaneous withdrawal, chase, and feed.

   In both field and captive studies, a fight was defined as any interaction involving one or more of the units forearms locked, pawing, hit, kick and the three pushing actions. RU fights typically extended over two or more bouts; i.e., sequences involving one or more of the
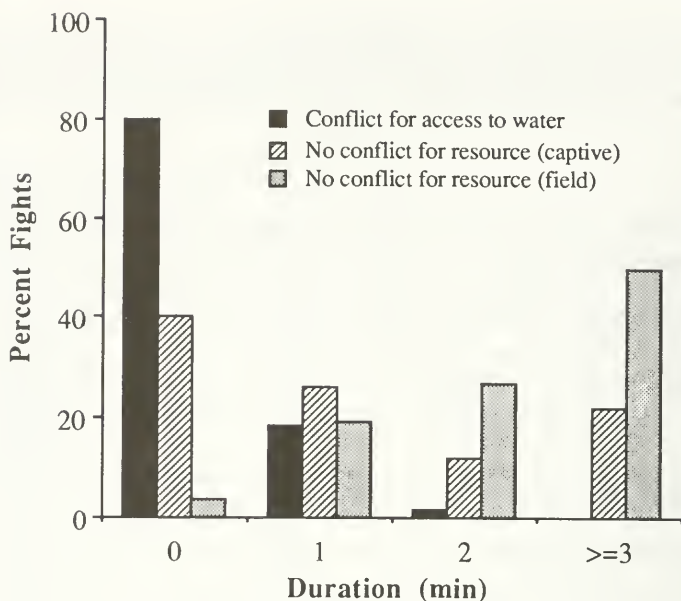
**FIGURE 2.** Comparison of the durations of RR fights over access to a resource (water) in the field, and RU fights where no access to a resource is disputed in the field and captivity.

above units were interrupted by pauses in which participants remained in physical contact or within close proximity ( < 2 m), usually standing or grooming. Thus, the duration of a fight was determined from the time of initial contact between the participants to the time of withdrawal of one or both to distances > 2 m. A bout was distinguished as a period in which one or both participants performed one or more of the characteristic fighting behaviours.

RESULTS

*Structure of Fights*

In the field, RU fights occurred between all age/sex classes except adult male-female dyads (Table 1). Fights were least frequent between females and most frequent between mothers and their male young-at-foot. Among males, fights were most common between medium-sized (20 - 60 kg) males; i.e., males which were sexually mature but inferior in competition for mates (Croft, 1981). Fights typically occurred over one or more bouts. Medium-sized males engaged in longer fights with multiple bouts relative to other dyads (Table 1).
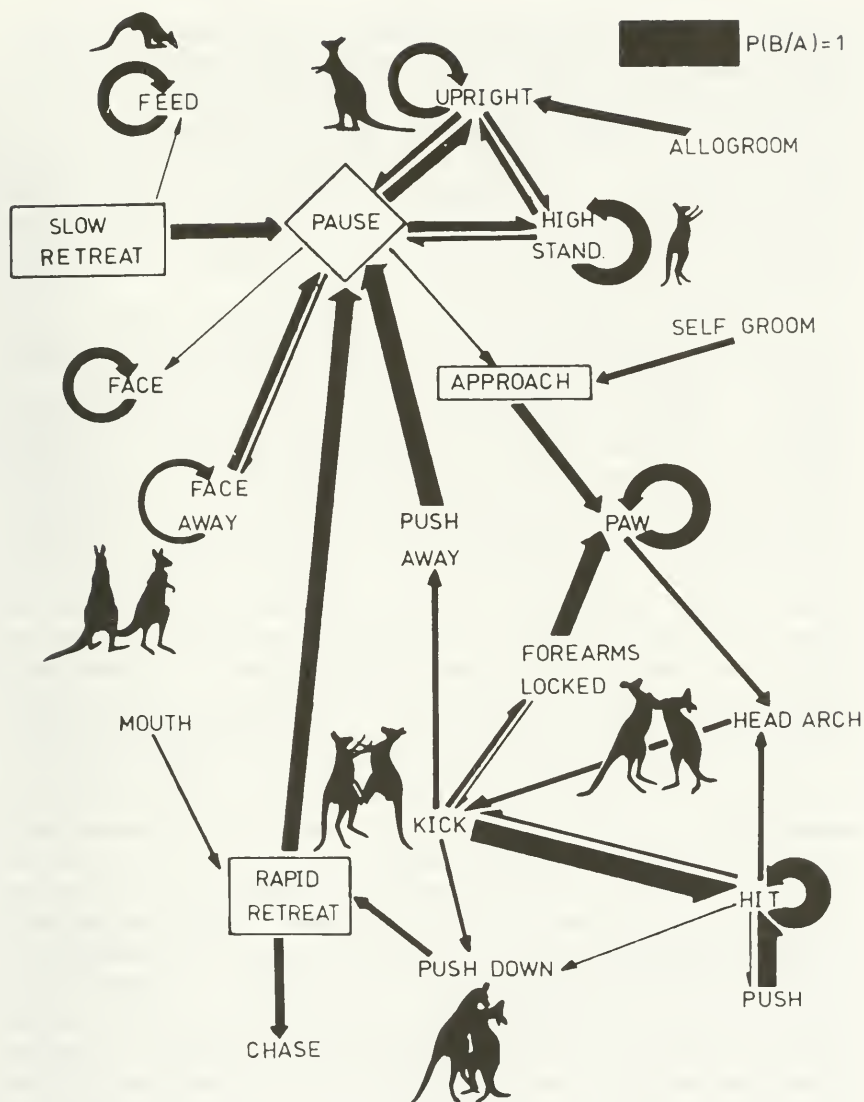
**FIGURE 3.** Significant positive transitions for inter-individual fight sequence derived from pooled data for 85 videotaped fights in captive group. Thickness of arrow indicates transition probability (P[B/A]).

To determine if structural differences occurred between fights involving a conflict over a resource (RR fights) and those not immediately resource-based (RU fights), RR fights at water in the field and RU fights in the captive group were analysed. Data on the duration of RU fights in the field were also used. There were clear differences.

RR fights at water were significantly shorter than those not involving resource competition (Figure 2), i.e., RU fights in either captive or field populations. Significantly more RR fights at water (76%, $n = 25$) were preceded by threat behaviour (i.e., stiff-legged walk, biting at sternum or full vertical body extension) than RU fights in the captive group (6%, $n = 85$) (Fisher Exact test, $p < .001$). In RR fights at water, the winner was significantly more likely to kick its opponent (83%, $n = 18$) than in RU fights in the captive group (19%, $n = 62$) ($X^2 = 18.03$, $p < .01$).

A number of other structural features of the RU fights in the captive group suggested that they were more analogous to play-fighting than to competitive fighting. A composite picture of the fight sequence was determined by combining the inter-individual behaviour sequence determined from the 85 RU fights recorded in the captive group (Figure 3). The core fighting behaviours are shown in the bottom right. The goal of the fight appears to be gaining a superior position to 'push down' the opponent leading to its rapid retreat. The most potent weapon of the kangaroo, the kick delivered with the full force of the hopping muscles, is not directly related to defeating an opponent. In fact, kicking may be employed as a retaliatory behaviour against the pushing thrusts of an opponent. Winners of fights push, push away, and push down significantly more frequently than losers, whereas the latter paw and kick significantly more frequently (Table 2). Losers were also significantly more likely to deliver the first (42/49 fights, Binomial test, $p < .001$) and last kick (41/49 fights, Binomial test, $p < .001$) in a fight. Thus, winners were not reserving a kick as a 'king hit' to terminate a fight.

The dominance relationships between the eight captive males were determined from success in supplanting interactions. The males were ranked in descending order as follows from the proportion of aggressive interactions (excluding fights) won (shown in parentheses): M1 (0.94), M2 (0.74), M3 (0.66), M4 (0.51), M5 (0.49), M6 (0.39), M7 (0.27), and M8 (0.21). In fights where kicking occurred, it was the subordinate (48 fights) that was significantly more likely to kick than the dominant (9 fights) (Binomial test, $p < .001$). Thus, the dominant individual appeared to be restraining its kicking behaviour while interacting with a subordinate in these RU fights which was not the case for at least the winners of RR fights as shown above. This form of possible 'self-handicapping' was further indicated by the stance adopted by larger individuals while fighting with smaller ones in RU fights. A measure of the percent difference in the time spent in an upright or highstanding posture for dominant and subordinate was calculated from percent difference $= 100*(D_d - D_s)/(D_d + D_s)$ where $D_d$ = time dominant spends in posture and $D_s$ = time subordinate spends in posture. If individuals were of the same size class then the

## TABLE 2
### Comparison of the Mean (± SE) Frequency per min of Behaviour shown by Winners and Losers in Videotaped Fights (*n* = 80) among Captive Males

| Behaviour | Winner | Loser | $Z^*$ | P |
|---|---|---|---|---|
| Winner > Loser: | | | | |
| Approach | 0.63 ± 0.10 | 0.61 ± 0.24 | 2.48 | < .05 |
| Selfgroom | 0.67 ± 0.14 | 0.32 ± 0.11 | 3.30 | < .001 |
| Face | 0.22 ± 0.06 | 0.10 ± 0.03 | 2.75 | < 0.01 |
| Upright | 1.55 ± 0.19 | 1.25 ± 0.21 | 2.50 | < .05 |
| Hit | 7.82 ± 0.63 | 6.87 ± 0.65 | 2.22 | < .05 |
| Forearm Lock | 1.13 ± 0.14 | 0.43 ± 0.15 | 4.15 | < .001 |
| Head Arch | 1.87 ± 0.24 | 0.98 ± 0.15 | 3.38 | < .001 |
| Push | 0.63 ± 0.11 | 0.24 ± 0.11 | 3.27 | < 0.01 |
| Push Away | 0.67 ± 0.17 | 0.31 ± 0.17 | 3.67 | < .001 |
| Push Down | 1.84 ± 0.24 | 0.59 ± 0.18 | 4.83 | < .001 |
| Feed | 0.62 ± 0.13 | 0.46 ± 0.12 | 2.16 | < .05 |
| Loser > Winner: | | | | |
| Paw | 3.65 ± 0.46 | 4.94 ± 0.40 | 3.12 | < .001 |
| Kick | 0.42 ± 0.20 | 1.64 ± 0.25 | 4.24 | < .001 |
| Slow Retreat | 0.11 ± 0.05 | 1.12 ± 0.22 | 4.97 | < .001 |
| Fast-Retreat | 0.10 ± 0.04 | 0.90 ± 0.19 | 4.22 | < .001 |

*Wilcoxon Matched-Pairs Signed-Ranks test and associated 2-tailed probability

difference between dominant and subordinate was negligible (Figure 4). However, if the opponents were of different size classes then the dominant spent more time in the upright posture and the subordinate in the highstanding posture thus bringing them to equivalent sizes.

Another feature of play-fights is that role reversals, either dominant/subordinate or attacker/defender, may occur (Hole, 1988). This structural feature for RU fights was examined from the perspective of reversals in dominant/subordinate roles. However, success in RU fights followed the dominance relationship between individuals. If they were of the same age class then dominants won (i.e., extracted a final retreat from the opponent) significantly more fights than subordinates (15/18 fights, Binomial test, $p < .01$). Likewise, when opponents were from different age classes, dominants won significantly more fights than subordinates (53/62 fights, Binomial test, $p < .001$). In five additional fights between different age classes no winner emerged. These results do little more than confirm that dominance in an agonistic context (supplanting) extends to another social context (RU fights). Thus, the question of reversals in RU fights was addressed in another way using multivariate analysis in order to take account of variation across all behaviour units employed. It was as-
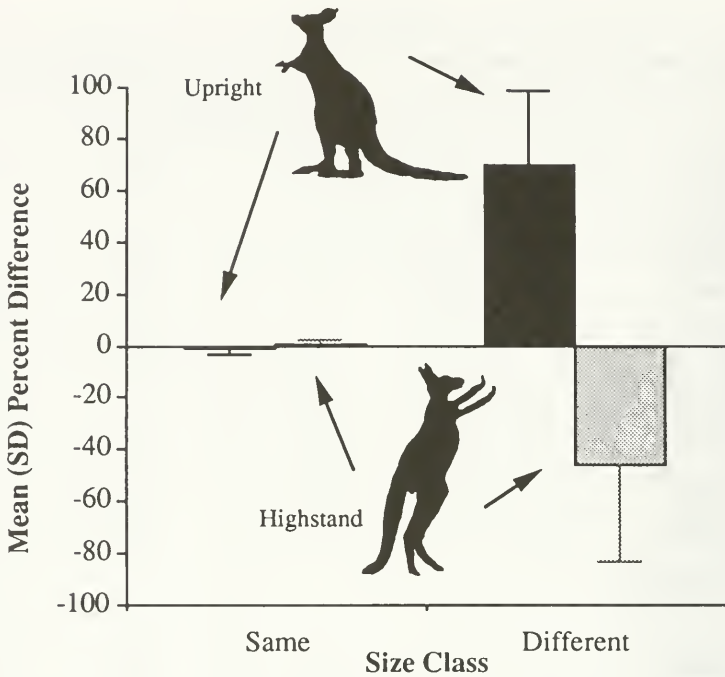
**FIGURE 4.** Relative durations of dominant and subordinate adopting upright or highstanding postures when they were of the same or a different size class.

sumed that the alpha-male's (M1) behaviour in fights typified the dominant strategy and that the gamma-male's (M8) behaviour typified the subordinate strategy. The behaviour of these two males was then used to classify the strategy employed by all other males in fights using a discriminant analysis (SPSS Inc., 1986). The data on frequency of behaviour units employed in RU fights were used but since the repertoire was large (25 units), the number of variables was reduced by factor analysis (SPSS Inc., 1986) before performing the discriminant analysis. The factor analysis extracted ten factors explaining 70% of the variance and the factor scores on these ten factors were used in the discriminant analysis. The resulting discriminant function correctly classified the fights of the alpha ($n = 17$) and gamma ($n = 23$) males. The function was then used to classify the remaining 130 fights as being either typical of the dominant or subordinate class and this classification was compared to the actual status of the individual performing the behaviour. Reversals were found for some individuals but a dominant was significantly more likely to behave as a dominant (60/85 fights, Binomial test, $p < .001$) than a subordinate and likewise subordinates behaved as subordinates (71/85

fights, Binomial test, $p < .001$). The assumption of a dominant/subordinate role in fights was not random (Kolmogorov-Smirnov, $p < .01$). In the majority of fights (49/85), the opponents assumed the correct dominant/subordinate roles. A reversal of these roles was rare (6/85 fights) but opponents commonly both assumed the same role (30/85 fights).

*Partner Selection*

The structure of RU fights suggests that individuals do not participate solely to exercise their dominance over another individual. Dominants self-handicap and opponents commonly behave in the same role whether dominant or subordinate. The red kangaroos invest time and energy in fights and may risk injury and, in the field, become more conspicuous and less vigilant to predators. Hence, it is fair to assume that this behaviour is advantageous to the participants. Various theories about the function of play predict that maximum benefits accrue when skills and physical strength are matched to maintain a stable play relationship (Fagen, 1981). Partner selection in 127 fights in the captive population was examined to look at such relationships.

The captive population contained four size classes of males. The frequency of fights between individuals of the same size class (26), or one (87), two (13), or three (1) classes smaller/larger was significantly different from those expected from the distribution of size class differences in the population (Kolmogorov-Smirnov, $p < .001$). The standardized residuals (SR) show that fights within the same size class were about as frequent as expected (SR = 1.89, ns). Fights with a partner one size class smaller or larger were significantly more frequent than expected (SR = 4.31, $p < .001$) but where the size class difference was two or three, fights occurred significantly less than expected (SR = -3.83, $p < .001$; SR = -4.01, $p < .001$; respectively). Thus partner selection tends to bias the outcome in favour of a superior opponent but as this disparity increases then fights become rare.

Partners may or may not derive equal benefits from fights. One opponent may exploit and bully the other or their relationship may be cooperative and beneficial to both. The relationship between kinship and fight partner selection was examined to illuminate these alternatives. The captive population comprised three classes: non-relatives, half-sibs and full-sibs. Fights with non-relatives were significantly more common ($n = 75$, SR = 2.54, $p < .01$) and those with half-sibs significantly less common ($n = 22$, SR = $-$ 2.59, $p < .01$) than expected, whereas those with full-sibs were about as common as expected ($n = 30$, SR = $-$ 0.52, ns). However, this result is confounded by possible size differences between partners which, as shown above,

significantly influenced partner selection. Even so, the same result holds for fights between opponents of one size class difference: non-relatives ($n = 58$, SR $= 2.47$, $p < .01$), half-sibs ($n = 3$, SR $= -4.05$, $p < .001$) and full-sibs ($n = 26$, SR $= 0.85$, ns). The trend was similar for other size class differences, but sample sizes were too small for robust statistical analysis.

*Disruptions and Takeovers*

One benefit of these RU fights may be to increase the skills and/or physical development of one or both partners. Therefore, it should be advantageous for a superior individual to disrupt this skill/physical development in a lower ranking individual which may later challenge its dominance status, or, to join in and so match skill/exercise increments. Likewise, more support may be given to the development of a close relative than to an unrelated individual. These possibilities were investigated by analysing fights where disruptions or takeovers occurred by a third individual. A disruption was defined as the intercession of a third individual into a RU fight between two opponents causing that fight to conclude abruptly. A takeover was defined as the displacement by a third individual of one of two opponents engaged in a RU fight followed by immediate initiation of a fight by that individual with the remaining opponent.

Most RU fights (72%) proceeded without a third individual interceding. Where fights were disrupted, the victim was significantly more often of lower than of higher rank to the intruder (14/16 observed, 7/16 expected; Kolmogorov-Smirnov, $p < .001$). Similarly for takeovers, the individual excluded was significantly more likely to be of lower rank to the intruder (19/20 observed, 8.5/20 expected; Kolmogorov-Smirnov, $p < .001$). Analysis at the individual level was not possible with the low frequencies observed but the alpha male interceded in 50% of the fights disrupted or taken over. An individual was more likely to stop the fighting of a non-relative ($n = 26$, SR $= 1.61$) than a half-sib ($n = 13$, SR $= -0.52$) or full-sib ($n = 9$, SR $= -1.34$) but these differences were not significant (Kolmogorov-Smirnov, ns).

## DISCUSSION

Fagen (1974) has divided the various approaches to the study of animal play into structuralist and functionalist camps. The structuralists maintain that play can be differentiated from 'serious' behaviour by its form. The most distinctive feature is usually a play-signalling behaviour. Red kangaroos engage frequently in fights

where no resource is in immediate contest and the form of these RU fights suggests that they are play-fighting. The behaviour is most common between younger males and between mothers and their male young, as found in other sexually dimorphic species (Symons, 1978), but is not confined to the juvenile phase. It is differentiated from RR fighting during conflict for a resource (specifically water) by its longer duration, and the absences of threat behaviour and damaging kicks. The latter two are the more distinctive characteristics since RR fighting for access to oestrous females may also be lengthy (Croft, 1981). Initiation of a RU fight may be a simple approach of one male to another, but both males often face each other and engage in grooming and scratching behaviour. They may mirror each other in these actions which, although they are not structurally different to grooming in other contexts, may serve to signal an intention to play without confusion with threat postures.

The tactical goal in RU fighting is to force the opponent off balance with vigorous pushing thus gaining a superior position to force it to retreat. Such goals are characteristic of play-fighting in other mammals (Symons, 1978). In general, the fighting behaviour shows many of the structural features considered to be distinctive in animal play (Bekoff, 1978). There is some lack of dominance distinctions, self-handicapping by the larger of two opponents occurs, threat behaviour characteristic of serious fights is absent, and potentially damaging behaviour is restrained. Thus, the context, the goals, and the structure of RU fighting all suggest that it is a form of play in red kangaroos.

Functionalists maintain that play can be differentiated from other behaviour only if it can be shown to be goal-directed and adaptive. Four functions that have been favoured are assessment, skill development/exercise, regulation of development rates, and socialization (Fagen, 1981).

Assessment is a mechanism for informing individuals of their relative fighting abilities and dominance ranks. In a relatively closed social system, such assessment will be applied to particular individuals. If kinship is recognised then two strategies might emerge. Firstly, if a play relationship is formed between unrelated individuals and results in an increase in fitness then each individual should behave selfishly to emerge dominant in the fight. A loser should stop fighting or attempt to injure its opponent. Secondly, for related play partners the strategy may be to accept the subordinate role and not injure a sib as that could decrease inclusive fitness. These two strategies do not clearly emerge in red kangaroo RU fighting. Partners are moderately different in size and unrelated more often than if they were chosen at random. Thus, the larger individual may be bullying an unrelated smaller one and thus reducing its chances of usurping

its dominance rank. Even so, the smaller individual may gain some benefit by testing itself against a superior opponent ranked above it. There was no evidence that either partner attempted to injure the other although kicking by the subordinate could fall into this category. However, if this kicking were to inflict injury then the dominant would not be expected to accept this fatalistically without severe retaliation. Some cooperation does occur in these RU fighting relationships in that the dominant handicaps itself but perhaps it could thereby be deceiving the subordinate as to its true abilities.

I favour assessment as being an important function of RU fighting in red kangaroos. In the wild, they have an open social system with little group stability and dispersal of males over long distances (Croft, 1981). Thus, assessment of other males' fighting abilities must be generalized rather than specific to certain individuals and this may explain why RU fighting as a form of play continues into adulthood. It may provide assessment with a low risk of injury as opposed to full confrontation in a potentially injurious fight. The results of this study provide no clear relationship between kinship and play partner selection or play behaviour. In an open social system this is probably unimportant. Only one young is reared in a year and so there is no litter-mate, and dispersal makes inbreeding unlikely.

Skill development is a likely outcome of play-fighting. It should improve the coordination of young individuals and the development of winning tactics. However, skill development alone does not explain why red kangaroos continue to play-fight throughout their life. In adulthood, learning about the skills of an opponent rather than learning and improving one's own skills would likely be more important.

Like skill development, exercise is an inevitable consequence of a rigourous activity such as play-fighting. Keeping the cardio-pulmonary and muscular systems in tone could therefore be a benefit of play-fighting. Generalized locomotory activity could serve a similar function without recourse to the complexities of interactional behaviour. Thus, exercise is no doubt a benefit of RU fighting but probably not the only benefit, and RU fighting is probably not the only way to gain the necessary exercise.

Socialization as a function of play implies the establishing and strengthening of social bonds and social cohesion through play behaviour. In red kangaroos where little group cohesion is evident this is unlikely to be an important function of play-fighting. As stated above, relationships are probably generalized to particular classes of individuals rather than specific known ones. This functional hypothesis has also been discredited because of its group selectionist connotations (Fagen, 1981).

Play-fighting in red kangaroos is neither truly cooperative nor disruptive and selfish. Fagen (1981) drew a similar conclusion in re-

viewing animal play in other species. As Fagen points out, the interests of play partners will rarely coincide. Each has its own requirements for experience in play and so a stable relationship will only form where there is some compromise between the partners' differing optima. Self-handicapping, lack of dominance distinctions, and role reversal are reflections of this. The darker side of red kangaroo play-fighting is expressed in the disruption of play-fights by a third interceding individual. Here it was shown that dominants, particularly the alpha male, reduce the play-fighting of lower ranks to some extent. This bullying may be to the higher ranked individual's advantage in delaying usurpation of their rank from below in the hierarchy. A corollary of this observation and the assessment hypothesis is that an alpha male in decline from age-related disabilities or injury should avoid play-fights with the lower ranks. Rejection of play-fight invitations were too infrequent in this study to analyse this. However, some observations on an eastern grey kangaroo (*Macropus giganteus*) group were also made at the Cowan field station (Croft, unpubl.). The alpha male in that group avoided fights with the beta male whenever the latter approached with invitational behaviour. Shortly after these observations, the beta male attacked the alpha one causing fatal injuries.

The 'boxing' behaviour of kangaroos intrigued and delighted the early European observers of the Australian fauna (e.g. Dahl, 1897). Man-kangaroo matches were an occasional diversion for the early colonists (Hornage, 1972). This study shows that these boxing matches in red kangaroos fulfill an important role in their social organization and should neither be viewed as potential death matches nor dismissed as human amusement. If we reflect on the consequences of our own school yard brawls, it is evident that play-fighting has an important influence on status and social development. In a sexually dimorphic species such as the red kangaroo, where competition between males for matings is intense, development and improvement of fighting skills and assessment of potential competitors will be important. Play-fighting provides an avenue for this without the high risks of injury in an escalated confrontation where kicks are the cut and thrust of the fight rather than a simple parry.

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