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pp. 173-186

     Author's note, May 2004: JMS was an incredibly stimulating individual. He was such an enthusiastic naturalist that we wanted to give him a few curious and peculiar behaviors to contemplate in his armchair in Sussex. The volume was a Festschrift, and this was our modest contribution to the celebration of a great mind.

13

Asymmetric contests in social mammals respect, manipulation and age-specific aspects

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Introduction

The application of game theory to the study of fighting behaviour has led to an important distinction being drawn between contests where the opponents have never met each other before, and contests where the opponents have interacted previously. In the former, each contestant may not be able to assess its chances of defeating its opponent; whereas in the latter, each contestant has prior information about the relative size, age, or motivation of the opponent. Thus in a stable social group, animals will be more likely to utilize asymmetries to settle contests without engaging in costly fighting (Maynard Smith, 1982). In this chapter, we will focus on the nature of asymmetries that are commonly found within groups of social mammals and we will show how these affect fighting behaviour.

First, we will describe how asymmetries in 'resource-holding power' (RHP, Parker, 1974) and in `ownership' are utilized, and how one asymmetry may take priority over another in different mammalian species. Second, we describe how individuals may `abuse' their opponents' respect of an asymmetry and may utilize complex behaviours in order to cancel an asymmetry. Finally, we will

discuss how in mammals age-specific asymmetries will typically include differences in RHP, payoffs and/or costs.

Asymmetries in RHP v. ownership

No two individuals have exactly the same competitive ability and most behavioural biologists are generally measuring differences in resource holding power (RHP) whenever they measure social dominance. Dominance `hierarchies' have been detected within age-sex classes of most group-living species, and considerable effort has been devoted to testing whether high dominance rank correlates with reproductive success. For our purposes, however, it is sufficient only to show that a subordinate animal will consistently defer to a dominant animal in a pairwise competition for a valuable resource, such as food or a resting site. Where such dominance relationships are conspicuous, by definition interactions between individuals are affected by an asymmetry in RHP. Contests are usually settled without costly fighting - the outcome instead depends on the recognition of the asymmetry.

However, in a number of species it has been found that individuals respect `ownership' of a resource, so that an animal with a resource usually will not be supplanted from the resource by another. Such `respect' of ownership is mutual: the `intruder' may be an `owner' during a subsequent interaction. A common example of respect of ownership among territorial animals is that an individual is dominant to a neighbouring conspecific while on his own territory, but he is subordinate while on his neighbour's territory (see Maynard Smith, 1982). When two individuals simultaneously become owners of the same territory, there is no asymmetry of ownership and both `owners' will fight intensely (e.g.. speckled wood butterflies, Davies, 1978).

Respect of ownership extends to other resources besides territories; particularly to receptive females or to certain kinds of feeding sites. In these cases, a dominant individual does not supplant an otherwise subordinate individual from the resource. In some cases, possession of the resource may of itself confer a competitive advantage, either because it is difficult to separate the animal from the resource (e.g.. copulating male dung flies, Parker, 1974) or because the resource is highly portable (e.g.. subordinate male baboons can carry away very small carcasses when confronted by a dominant male whereas dominant males supplant subordinates from large carcasses (Hamilton & Busse, 1982)). However, `respect' of ownership can evolve even when ownership does not confer a competitive advantage or involve an asymmetry in payoff (see Maynard Smith & Parker, 1976).

Male Hamadryas baboons restrict the movements of females and thus form stable one-male `harems'. Experiments by Kummer and colleagues (Kummer, Gotz & Angst, 1974; Bachmann & Kummer, 1980) have shown that (i) male-male fighting for females is common only when two males are simultaneously presented with an unpaired female, (ii) if one male comes into contact with the female only a few minutes before a second male, the second male will respect the first male's ownership of the female, (iii) respect is mutual within pairs of males; one may be an owner on one occasion and a rival on another and (iv) dominant males respect ownership of subordinate males, *except when differences in RHP are extreme.*

More interesting, however, than the respect of what would ordinarily be long-lasting or permanent relationships where females may be expected to maintain the status quo (Clutton-Brock & Harvey, 1976), is the respect of `temporary ownership' of oestrous females within social groups. In many species living in groups with more than one breeding male, one male will monopolize

an oestrous female by maintaining a close proximity to her, preventing her from moving towards other males, and threatening other males if they come close to the female. These 'consortships' last from a few hours to days (sometimes over the entire oestrous period), but a number of different males may consort with the same female in the same or subsequent oestrous periods. In a study of olive baboons, Packer (1979b) found that dominant males would defer to subordinate males while the subordinates were consorting. Consequently the mating success of subordinate males was greater than would be expected if RHP were the only variable affecting mating success. However, respect of ownership did not completely overcome differences in RHP, since low-ranking males started consorting earliest in the female's cycle but the highest ranking male had usually gained control of the female by the time she was most likely to conceive. In this study, `dominance' was based on each male's ability to supplant other males from feeding sites and hence reflected `RHP' of food.

In Table 1 we contrast the relative importance of asymmetries in RHP and respect of ownership in competition for key resources in three mammalian species: the African lion, the olive baboon, and the chimpanzee. We compare males in each species during competition for access to oestrous females, and we compare females in competition for food. All three species live in stable social groups with multiple breeding females and males. In all three, males form temporary consortships with oestrous females, and no one male is able to monopolize all of the matings with oestrous females. In both lions and baboons, females often feed together and competition for access to food is common. Female chimpanzees only infrequently feed together, but competition for food has been observed.

The three species vary in the extent to which ownership is respected. Lion males are conspicuous in the extent to which they respect their companions' temporary ownership of females (Packer & Pusey, 1982). Fighting only occurs when ownership is unclear or when two consorting males come into close proximity. In contrast, a dominant male chimpanzee can apparently displace another male from a female and successful consortships by subordinate males require both that the female cooperates with the male and that the pair remains hidden from more dominant males (Nishida, 1979; Tutin, 1979; Tutin & McGinnis, 198 1). Olive baboons show some respect of ownership (see above), but in most groups high-ranking males are disproportionately successful. Therefore, male lions apparently show the `Bourgeois strategy' (Maynard Smith, 1976), whereas male chimps rely more exclusively on RHP assessment, and male baboons are intermediate between the other two species.

For the Bourgeois strategy to be an `evolutionarily stable strategy' in a population of `hawks' and `doves', the average costs of injury during an escalated fight should exceed the average payoff from winning (Maynard Smith, 1976). It would therefore be expected that the extent to which each species shows Bourgeois behaviour varies either because the costs of fighting are higher in some species than in others or because the `value' of an oestrous female is lower. Although precise data on costs of injury are unavailable, there are obvious differences in the three species in the degree of weaponry. Lions have well-developed biting dentition and powerful claws, and male baboons have enlarged canine teeth which they keep razorsharp by honing them against their premolars (Simons, 1972). A lion can easily kill another lion, and male baboons can inflict serious wounds in one-on-one fights (see Table 1). For their body size, male chimps have less-welldeveloped canines than do cercopithecine monkeys (Harvey, Kavanagh & Clutton-Brock, 1978), and serious wounds are mostly inflicted during gang attacks rather than one-on-one fights (Goodall *et al.,* 1979).

173

Table 1. *Factors affecting respect of ownership in three species*

	Lions	Baboons	Chimpanzees
Males			
A. Extent to which temporary ownership of oestrous females is respected (see text)	High (1)[a]	Moderate (2)	Low (3–5)
B. Chances of being injured during one-on-one fight	High (1, 6)	Moderate (2, 7)	Low (8)
C. Percentage of oestrous periods leading to conception	20–28% (6, 9)	16% (2)	13–20% (5, 10, 11)
D. Percentage of pregnancies leading to young surviving to breeding age	14–44% (12, 13)	c. 60% (14)	c. 40% (5, 8)
E. Average litter size	2.5 (6)	1 (14)	1 (8)
F. Value of oestrous female $= C \times D \times E$	0.07–0.32	0.10	0.05–0.08
G. Differences in age/size of males in same group	Low: typically of similar age (1)	High: range 8–25 y (2, 14)	High: range 16–34 + y (8)
Females			
A. Extent to which temporary ownership of feeding site is respected (see text)	High (6, 15, 16)	Low (17)	Low (4, 11, 18)
B. Chances of being injured during one-on-one fight	High (6)	Low (17)	Low (8, 19)
C. Value of specific feeding site (see text)	Moderate	Low	Low?
D. Differences in age/size of females within group	Moderate: some groups all same age, others show range of 4–16 y (16)	High: range 5–25 y (14)	High: range 13–34 + y (8)

[a] References: 1: Packer & Pusey, 1982; 2: Packer, 1979a; 3: Tutin, 1979; 4: Nishida, 1979; 5: Tutin & McGinnis, 1981; 6: Schaller, 1972; 7: Packer, 1977a; 8: Goodall, 1983; 9: Packer & Pusey, 1983; 10: Teleki, Hunt & Pfifferling, 1976; 11: Pusey, 1978; 12: Bertram, 1975; 13: Hanby & Bygott, 1979; 14: Packer, Goodall & Sindimwo, unpublished; 15: Bertram, 1978; 16: Packer & Pusey, unpublished; 17: Hausfater, 1975; 18: Pusey, 1983; 19: Goodall, 1977.

We have estimated the `value' of an oestrous female in each species given the probability of conception and survivorship of young. The likelihood that a given oestrous period will lead to a surviving offspring is quite similar in all three species (Table 1). Therefore, the difference in the extent of Bourgeois behaviour in the three species is more likely to be due to differences in costs of fighting than to differences in payoffs.

An additional factor, however, might be the different age structure typical of males in the three species (Table 1). Male lions are often closely matched in age and size, whereas male baboons and chimps are often of quite different ages. As a result differences in RHP will typically be smaller in lions and therefore respect of ownership will be more likely to occur (Hammerstein, 1981). Where male lions are not equally matched, males of apparently lower competitive ability also have lower mating success (Packer & Pusey, 1982). However, we do not yet know if this is because inferior males are less likely to gain access to females in the first place, or because their superior companions displace them from their consort partners. Male baboons are not typically matched in age, yet they are intermediate between the other two species in the extent to which they show respect of ownership. This suggests that high costs of fighting as well as age/size discrepancies must be involved.

Respect of ownership is often taken by field workers as evidence that there is an asymmetry in payoff or RHP biased in favour of the owner. However, we doubt that being the temporary owner of an oestrous female in these three species involves either a higher payoff or a lower risk of injury to the owner than to the rival. Packer (1979b) previously suggested that a consorting male would always have a higher payoff than a rival, assuming that the nth male to consort with the female has a $1/n$ chance of fathering the offspring, whereas the $(n + 1)^{th}$ male has only a $1/(n + 1)$ chance. This analysis is probably incorrect because both males are competing for exactly the same opportunity to fertilize the female over the next few hours or day (G. A. Parker & J. Maynard Smith, personal communication). Bachmann & Kummer (1980) showed that the preferences of females have some effect on the rivals' respect of ownership. A female that does not cooperate with the `owner' can be taken over more easily by a rival. However, of the species listed in Table 1, pairs of male lions and baboons showed mutual respect when each consorted with the same female on different occasions (Schaller, 1972; Packer & Pusey, 1982, and unpublished data) and in chimpanzees, where females' preferences seem to be *most* important to a consortship being successful, ownership is *least* important. Therefore, differences in the behaviour of oestrous females of the three species probably do not account for the varying extent to which ownership is respected.

The lower half of Table 1 compares the extent to which females of the three species respect another female's `ownership' of a feeding site. Female lions are as Bourgeois at the dinner table as their husbands are in the bedroom. We have never seen an adult female supplant another female from a kill in over 100 h observation of lions feeding together (Packer & Pusey, unpublished). In contrast, female baboons habitually supplant subordinate females from feeding sites and the few available data on female chimps show no evidence of respect of ownership. It is much more difficult to estimate the value of a feeding site except that it is probably highest to a female lion since she can less easily find an alternative feeding site and could starve if excluded by more dominant females from only a few consecutive kills. In fact, dominance orders at kills are undetectable in female lions (Schaller, 1972; Bertram, 1975; Packer & Pusey, unpublished). Again, costs of fighting will be highest in female lions and low both in female baboons and chimps (Table 1). Even a relatively

small female lion could inflict a fatal wound on a female conspecific - whereas this is very unlikely in baboons or chimps.

One difficulty in comparing female lions with the two primate species is that a lion's claws enable it to hold on to a carcass as well as injure a competitor and thus a positional advantage of ownership may be involved. However, this can not be the whole story since a female lion will relinquish a kill to an adult male without a fight (Schaller, 1972; personal observation); probably because a male lion is 40% heavier than a female.

The degree to which ownership is respected in these three species does not appear to depend on the degree of kinship between the opponents: individuals within each sex are typically related, except for male baboons (Packer, 1977a, 1979a) and female chimpanzees (Pusey, 1979). Furthermore, temporary ownership of oestrous females is respected by male lions both when the males are close relatives and when they are unrelated (Packer & Pusey, 1982).

We feel that these comparisons are valid, even though we have largely contrasted a carnivore with two primates. Other species of social carnivore show little if any respect of ownership. There is anecdotal evidence from both wild dogs and spotted hyenas that dominant individuals can supplant subordinates from receptive females and from food (van Lawick & van Lawick-Goodall, 197 1; Kruuk, 1972; Frame *et al.,* 1979). These two species differ from lions in that they lack vicious claws though they do have sharp teeth.

In summary, there are striking differences across species of mammals in the extent to which ownership of a resource is respected. These differences are probably due to variation both in the risks of injury from fighting and in the extent to which differences in RHP exist within social groups.

Manipulating asymmetries

Having seen that respect of ownership can sometimes override differences in RHP, we will now describe how individuals may manipulate their opponents' respect of ownership or other asymmetry, and how cooperative behaviour may often evolve in order to overcome ownership.

Asymmetry `abuse'

An individual is taking advantage of an opponent's respect of ownership whenever he behaves like an `owner' in order to avoid a fight, but the `resource' he is holding has no immediate value. For example, when a male baboon is being threatened by another male he will sometimes seek out a female that is not at the height of oestrus and `consort' with her, and his opponent will stop threatening him (Packer, 1979a,b). The `consorting' male's `ownership' of the female is respected, even though the female has no immediate value; and the `consorting' male ceases to show further interest in the female once his opponent has moved off. Thus, respect of ownership extends to situations where the aggressive interaction had not initially involved that specific resource, and a male may manipulate an opponent's respect of ownership to his own advantage.

Another asymmetry that apparently does not directly involve a resource is the carrying of infants by male baboons. While a male is carrying an infant in an encounter with another male, he is less likely to be threatened by and is more able to displace the other male, than when he is not carrying an infant (Packer, 1980). This behaviour probably originates from the protection of an infant by its father against a potentially infanticidal male (Busse & Hamilton, 1981). However, such `protection' is an insufficient explanation of the behaviour in contemporary populations. Males seek

out infants while being threatened by other males (Packer, 1980; Stein, 1981) and in one population the carrying male was more likely to have been the infant's father than was the opponent in only 39.7% of cases (N=161 cases of infant carrying, where data were available on the males' mating activity with the infant's mother at the time of conception (Packer, personal observation)). More important than the pattern of kinship between infant, carrying male and opponent is the fact that males generally carry infants during encounters with more dominant males (Ransom & Ransom, 1971; Popp, 1978; Packer, 1980; Collins, 1981; Stein, 1981). Thus, carrying an infant temporarily overrides differences in RHP in the same way as does respect of `ownership' of an oestrous female.

Therefore, carrying of infants may be another example of an individual manipulating an asymmetry in order to take advantage of his opponent's recognition of that asymmetry. Initially the behaviour may have functioned exclusively to protect the infant from infanticide. The usual explanation for infanticide by males is that by killing a female's young she will return to sexual receptivity more quickly (Hrdy, 1974). While protecting his infant, the father would be fighting for a high payoff - survival of his offspring - whereas the opponent would only be fighting for a chance to mate with its mother. We suggest that, once widespread, the respect of the asymmetry in payoff as signalled by carrying an infant was `exploited' by subordinates. Males actually compete for access to infants and the carrying of infants has become the source of considerable infant mortality in some populations (Collins *et al.,* 1984).

Both of these examples apparently involve exploiting an opponent's respect for asymmetry. In neither case, however, does it seem that the `abuse' is specifically used to gain access to a resource nor does it result in a permanent rise in dominance ranking (Packer, 1979b), but it is instead used to prevent the male from being threatened further. Therefore, if two males were having a dispute for some other reason, the male that suddenly consorts with an infertile female or that picks up an infant does so to `turn off' his opponent's attack. By creating a situation that has no worthwhile payoff to the opponent, he has made it no longer worthwhile for the opponent to risk injury. The `abusive' male benefits only by avoiding injury. As long as no resource is at stake, these behaviours need not be viewed as bluff. However, if the `abusive' male did occasionally use them to gain a resource it might be expected that they would be less likely to persist in the population (Andersson, 1980). These ideas are obviously speculative, but suggest the possibility that quite complex behaviours involving the creation of `asymmetries' may be used to settle contests in ways not previously appreciated.

Overwhelming ownership

In section 1 we showed that the respect of ownership can overcome differences in RHP, *unless differences in RHP are extreme.* An obvious technique whereby an individual may create an extreme difference in RHP is to form an alliance with a partner and to challenge an opponent cooperatively. Cooperative pairs of subordinate male baboons can easily displace a single, highly dominant individual (DeVore, 1962) and pairs of male baboons can also separate a consorting male from an oestrous female (Packer, 1977a). Hence, cooperating individuals overcome the asymmetry of ownership by greatly increasing their combined RHP in comparison with an owner. There are a number of examples of cooperation enabling individuals to overcome ownership: nomadic bands of male langurs can cooperatively evict a breeding male from his troop (Sugiyama, 1965; Hrdy, 1974), large coalitions of male lions can

173

evict smaller resident coalitions from prides (Bygott, Bertram & Hanby, 1979), and large groups of primates can expand the size of their territories at the expense of smaller neighbouring groups (see Wrangham, 1980).

Age-specific asymmetries

The life history of an animal as long-lived as most mammals is obviously complex, and is especially so in species living in groups comprised of individuals of different ages. Contests with different opponents may involve different asymmetries in RHP, different effects of injury on fitness, and different values of the resource.

It is already widely recognized that RHP will change with age in species where RHP is related to body size. In consequence, young individuals may adopt alternative strategies until they are large enough to become successful competitors. For example, some young male elephant seals successfully avoid direct competition with larger adult males for access to females by `sneaking' into harems (Le Boeuf, 1974). Because of their small size and lack of secondary sex characteristics, they are apparently difficult to distinguish from adult females.

It would also be expected that ageing animals will be more willing to engage in a serious fight since they are nearing the end of their lifespan anyway and thus have less to lose from sustaining a permanent injury (e.g. Popp & DeVore, 1979). Therefore, animals may show an increased `irascibility' when nearing senescence in the same way that females are expected to invest most heavily in their final offspring (e.g. Pianka & Parker, 1975). Meat is an unusual, but highly prized food item for chimpanzees, and ageing males will compete vigorously to gain access to meat (Wrangham, 1975). Older males thus gain or maintain access to meat more often than would be predicted from their usual dominance relations.

Recent studies have also suggested that the value of a resource will depend on the age of the contestant. For example, in many vertebrates young animals must rapidly gain weight in order to survive their first winter (e.g. yellow bellied marmots, Armitage & Downhower, 1974). Thus, access to a particular food item may be more critical to the survival of a yearling than to an adult (Barkan, Craig & Brown, 1982). **In** wild dogs, immatures have priority of access to meat and will aggressively displace adults from kills (van Lawick & van Lawick-Goodall, 1971; Schaller, 1972). While this must largely reflect the provisioning strategies of the adults, priority of access by yearlings persists even when subsequent litters are born (Malcolm & Marten, 1982). Since yearling dogs are apparently more subject to starvation than are adults, priority of access by yearlings may result from yearling `dominance' due to an asymmetry in payoff (Barkan *et al.,* 1982).

However, higher payoffs to younger animals have to be countered by the fact that wounds received while young may lead to a permanent loss in competitive ability. Thus the precise effects of fighting on lifetime reproductive success need to be considered. We will discuss the following example in detail in order to emphasize the importance of considering precisely how the costs of fighting will affect lifetime reproductive success (see also Caryl, 1980).

Males in most mammalian species disperse from their natal group or areas (Packer, 1979a; Greenwood, 1980) and in some, dispersal often does not occur until after males reach full size. In such exogamous species, males that bred with close genetic relatives would have offspring of lower average viability due to inbreeding depression (see Rails, Brugger & Ballou, 1979; Rails & Ballou,

173

1982). Therefore, when competing for access to mates, a male closely related to an oestrous female would have a lower expected payoff than a male less closely related to the female.

Full-sized male baboons still residing in their natal troop will not compete aggressively against immigrant males for access to oestrous females even though such `natal males' often compete successfully against immigrants for access to feeding sites (Packer, 1979a). This disparity in competitive behaviour for access to the two resources is not simply due to a higher value of food to the younger male (as suggested above) because males of similar age compete vigorously for females after they have emigrated and males that return briefly to their natal troops cease competing for females until they leave again. Although males might mate surreptitiously with females in their natal troop, they never defend their exclusive access to the female in the way typical of immigrant males.

Could the payoff asymmetry account for this behaviour? Packer (1977b) modelled the lifetime reproductive success of males as follows. A male baboon was assumed to be at the peak of his competitive ability when he reached full size, but he did not emigrate until a fixed time after this age. Competitive ability was assumed to determine the probability of winning fights against all opponents, but declined linearly as a function of the number of fights the male had engaged in. A continuous decline in competitive ability is expected due to the steady accumulation of scar tissue and loss of mobility due to wounding. Each male has a finite lifespan and, after the onset of senescence, the probability of fighting success declines rapidly to zero irrespective of the subsequent frequency of fighting. Each individual was viewed as having two phases to its lifetime - before or after emigration - and the payoff to gaining access to females before emigration is lower than after emigration. Each male could either behave as a `hawk' (competing aggressively for access to females) or a `dove' (deferring to a `hawk', and only gaining access to females in competition with other `doves'). Only hawks suffer a loss in competitive ability from fights and only when fighting other hawks. A male could show the same or a different strategy before and after emigration.

It was shown that the strategy observed in the wild, `play dove while in natal troop, play hawk after emigrating', could in fact be an evolutionarily stable *lifetime* strategy, but only when (i) the rate of decline in fighting ability was sufficiently high that a male that waited until emigration to play hawk would still be likely to `use up' most of his fighting potential before reaching senility, or (ii) when levels of inbreeding depression were severe (Packer, 1977b).

Otherwise the male should always play hawk both before and after emigrating. In any case, the best strategy for a male would obviously be to emigrate as soon as he reached full-size, as is often the case (Packer, 1979a). Males that remained longer in the natal troop apparently did so because they were subject to unusually high levels of aggression while attempting to join nearby troops.

Conclusions

There are striking differences across mammalian species in the extent to which `respect of ownership' influences competitive encounters. In broad agreement with predictions generated by Maynard Smith's analyses of the Bourgeois strategy, respect of ownership appears to be of greatest importance in contests where fighting is most costly. It is possible that animals sometimes `abuse' their opponents' respect of an asymmetry such as ownership, and the advantage of ownership is often overcome by opponents challenging an owner cooperatively. Complex life-history strategies typical of mammals and other vertebrates may be profitably interpreted by considering age-specific changes in RHP, potential costs of injury, and payoff from gaining access to a particular resource.

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173

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